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This document is part of a collection that serves two purposes. First it is a public archive for data and documents resulting from evolutionary, ecological, and behavioral research conducted by the Ketterson-Nolan research group. The focus of the research is an abundant North American songbird, the dark-eyed junco, *Junco hyemalis*, and the primary sources of support have been the National Science Foundation and Indiana University. The research was conducted in collaboration with numerous colleagues and students, and the objective of this site is to preserve not only the published products of the research, but also to document the organization and people that led to the published findings. Second it is a repository for the works of Val Nolan Jr., who studied songbirds in addition to the junco: in particular the prairie warbler, *Dendroica discolor*. This site was originally compiled and organized by Eric Snajdr, Nicole Gerlach, and Ellen Ketterson.

Context Statement

This document was generated as part of a long-term biological research project on a songbird, the dark-eyed junco, conducted by the Ketterson/Nolan research group at Indiana University. For more information, please see IUScholarWorks (<https://scholarworks.iu.edu/dspace/handle/2022/7911>).

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THE ECOLOGY AND BEHAVIOR
OF THE PRAIRIE WARBLER
DENDROICA DISCOLOR

ORNITHOLOGICAL MONOGRAPHS

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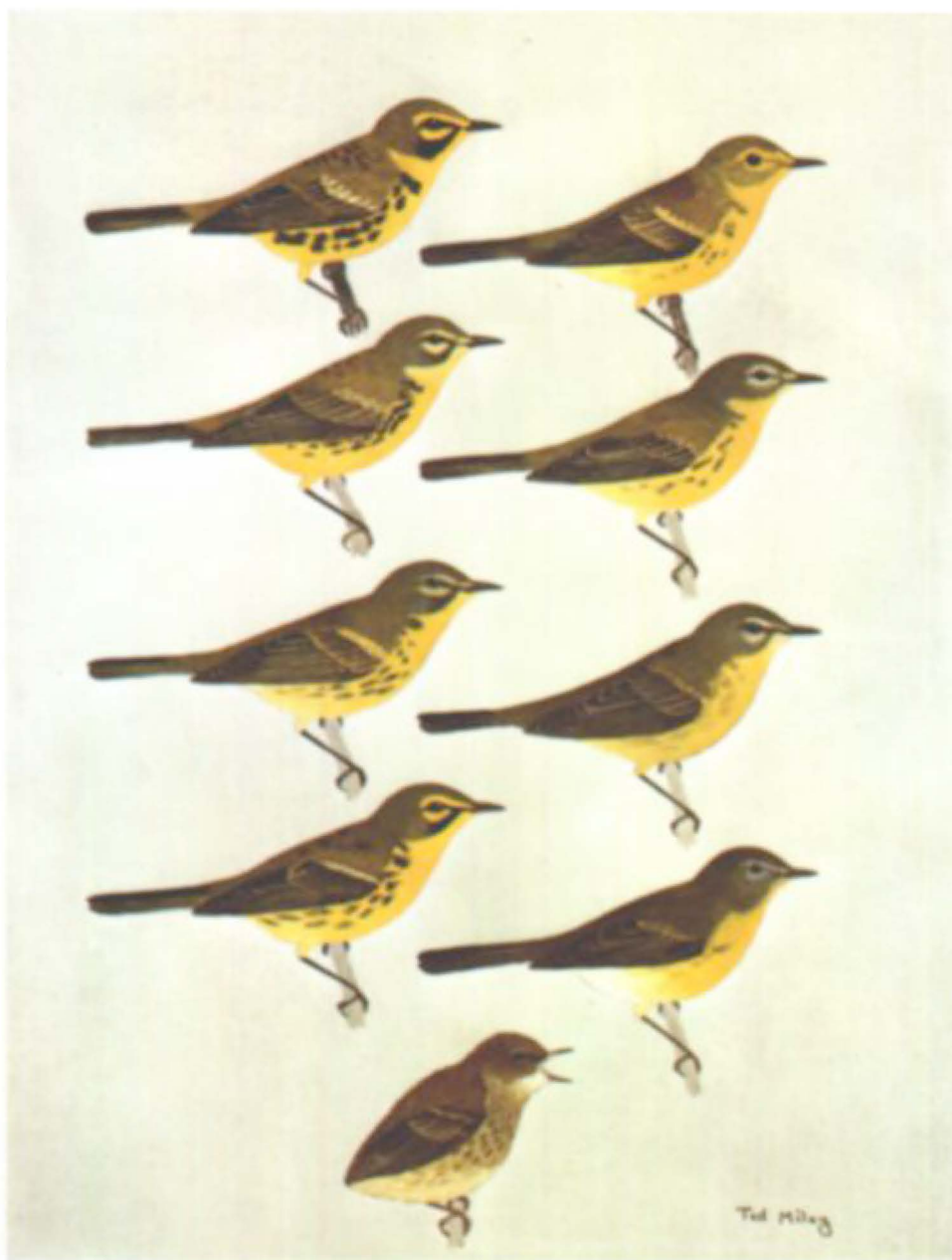
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FRONTISPIECE: Some plumages of the Prairie Warbler. Left column (top to bottom): FM 150432, spring, male older than 1 year; FM 69595, spring, 1-year-old male; FM 150438, fall, immature male; UMMZ 131336, fall, adult male. Right column: FM 150447, spring, female older than 1 year; FM 150449, spring, 1-year-old female; FM 150477, fall, immature female; FM 150435, immature female (?), postjuvenile molt. Bottom: UMMZ 67509, fledgling (male) at nest-leaving.

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BY
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Department of Zoology
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The American Ornithologists' Union
dedicates this volume
to the memory of one of its Benefactors
MARCIA BRADY TUCKER
Whose generosity launched this series of
Ornithological Monographs fifteen years
ago, and whose continued support,
until her death in December 1976,
made the series possible

*To my wife Sue and my friend
Margaret Nice—V.N.*

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INTRODUCTION

Dates, locations of study.—This study began in 1952, and systematic field work continued through 1965. Efforts to fill gaps in information continued until 1972.

The original study area consisted of a series of disjunct old fields totaling about 50 ha in area. These were surrounded by woods and/or cultivated land and lay in Monroe County, Indiana, in Sections 26, 27, and 34 of Township 9 north, Range 1 west of the second principal meridian. This area is referred to as "the University Farm" (Fig. 1). Construction of a golf course and a highway began in 1954 and by 1955 had destroyed the Prairie Warbler's shrubby habitat in the largest, central fields. Consequently, in 1955 and 1956 field work focused on prolonged observations of a few pairs occupying peripheral remnants of habitat. Beginning in 1957, attention was shifted to "the Griffey Tract," in which there were also about 50 ha of old fields. This tract lay northwest of the University Farm in Sections 21 and 22 of the township and range mentioned above (Fig. 1). Both study areas were just north of the city limits of Bloomington, Indiana, their center at about 39° 11' N, 86° 32' W.

Climate.—Mean annual precipitation at Bloomington is 111.9 cm. (Climatic information is taken from U.S. Department of Commerce Weather Bureau 1959 and is based on the period 1931–1955.) Mean rainfall during the months of the Prairie Warbler's presence (mid-April to mid-October) is rather evenly distributed, with the greatest monthly mean (12.4 cm) in June and the least (7.1 cm) in October. Vegetation begins to dry conspicuously in July in some years, not until September or October in others.

Mean annual temperature is 13°C. Monthly means, from April through October in chronological order, are 12.5, 18.1, 23.2, 25.3, 24.2, 20.5, and 14.5°C. Percentage of possible sunshine can be estimated by averaging monthly percentages from Indiana weather stations located northeast and southwest of Bloomington: April, 54%; May, 61%; June, 67.5%; July, 73.5%; August, 75.5%; September, 74%; October, 70.5%. During the approximately 6 months the Prairie Warbler is present, clear, cloudy, and partly cloudy days are about equally frequent, with the last of these occurring a little more often. In May and June, when most warbler nests are built, cloudy days are about as numerous as all other days combined.

Prevailing winds are from the southwest during most of the period April–October. Estimating their strengths at Bloomington from data recorded at other Indiana weather stations (see above), mean hourly speeds range from about 5.4 to 11.4 knots. Relative humidity at noon ranges from a mean of about 52% in October to about 57% in June.

Topography, vegetation.—The topography of the study areas was hilly, and Prairie Warbler territories had no standing water except for small puddles after rains. Old fields were separated by steep wooded ravines, some containing tiny streams, and many territories were small patches (as small as 1.5–2 ha) of shrubland at the ends or on the slopes of ridges (see Fig. 2). Extremes of elevation of land on or closely adjoining the study areas were about 274 and 183 m above sea

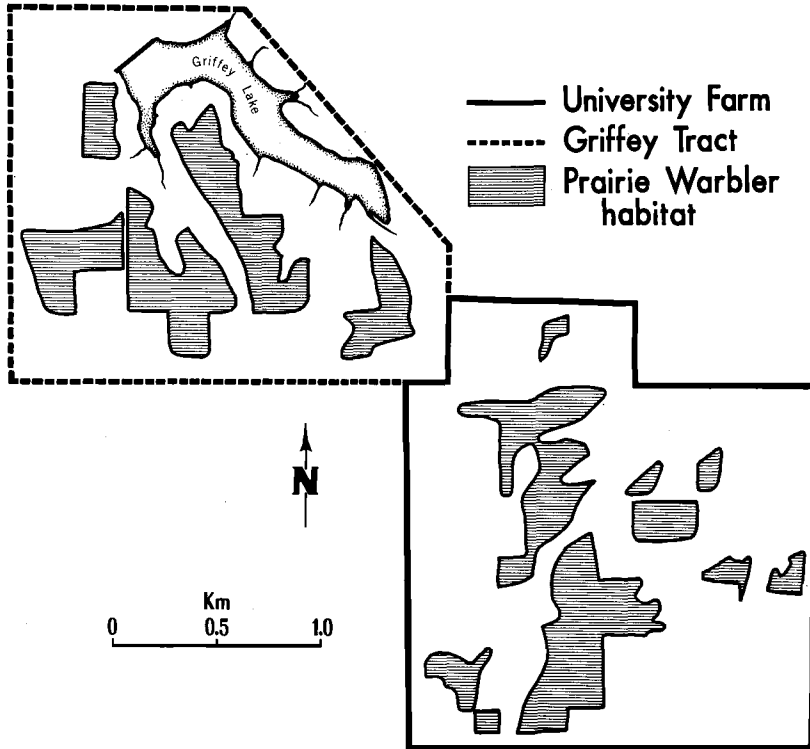


FIGURE 1. Positions of the University Farm and Griffey study areas. See text.

level. Erosion had stripped some areas of top soil, and they supported little plant life. Limestone outcropped on steep slopes, and on flatter surfaces sinkholes varying from 1–2 m to 30 m in diameter were rather common. The unglaciated topography was typically karst.

The age of the old-field vegetation on the University Farm varied from some 5 years to probably 15–20 years. Although parts of the larger of these fields appeared to have been mowed a few years before 1952, many invading trees had been left undisturbed. In some fields a few rows of Black Walnut, Black Locust, Jersey Pine, and White Pine had been planted, beginning in 1947, to control erosion. Much of the University Farm was only several years away from the time at which forest would have closed over it, had succession been allowed to continue. The species of its commonest trees and further details about the configuration of the vegetation can be inferred from data in Chapters 15 and 29.

The central fields of the Griffey Tract, acquired by the City of Bloomington to protect its water supply, ceased to be farmed in about 1946. Succession was at a much earlier stage than on the University Farm, as is evident from data in Chapter 29, from Figure 2, and from Figure 3. Descriptions of the vegetation by Nolan (1963) and Thompson and Nolan (1973) are supplemented by analyses in Chapters 15 and 29.

Distribution of field time.—Throughout the study all territories on the University Farm or Griffey Tract were visited virtually daily from early April, before Prairie



FIGURE 2. Aerial photograph of the Griffey Tract, July 1958. The fields south of the lake were the principal Griffey fields; compare Figure 33. Note topography and characteristic small openings in woods, which are often inhabited by Prairie Warblers.

Warblers arrived, until breeding ended in July or August. In several years daily field work continued into October. The amount and distribution of time spent in the field is indicated by computations covering 1952–1963. From 15 April through 20 July of those years, hours in the field from dawn through 0830 numbered 1381; from 0830 through 1230, 2326; from 1230 through 1630, 1044; and from 1630 until darkness, 773 (total 5524 hours). These figures include time spent by Joseph B. Board, Jr., and William E. Ryckman, who assisted me in prolonged observations of nests in 1956 and 1957. After 20 July 1952–1963, about 75% of 1298 hours of field time fell between 0830 and 1230.



FIGURE 3. Appearance of fields inhabited by Prairie Warblers. The upper photograph, taken 18 April 1958 by Gerald N. Svetanoff, is of a Griffey field. The lower photograph, taken 15 June 1954 by Duane Carmony, is of a University Farm field. As the study continued and succession progressed, Griffey vegetation came to look like that of the University Farm.

Abbreviations and other conventions used in text.—The usual metric-system abbreviations are used. Most statistical terms are spelled out; but SD is used for standard deviation, df for degrees of freedom, C for coefficient of variation, and *P* for probability. When probability statements would vary according to whether the test was one- or two-tailed, two-tailed probability is indicated unless the contrary is stated.

Many museum skins were made available for my inspection; specimens are referred to by abbreviations or initials of their institutions and label numbers. Initials used in this way are as follows: Smith. Inst., Smithsonian Institution; AMNH, American Museum of Natural History; USNM, United States National Museum (some specimens are labeled USNM-BS); CNHM FM, Chicago Natural History Museum; CM, Carnegie Museum; ROM, Royal Ontario Museum; CI M, Cleveland Museum; UMMZ, University of Michigan Museum of Zoology; USFWS, U.S. Fish and Wildlife Service.

Statements about behavior of individual birds from day to day or over greater periods of time, i.e. statements indicating that particular individuals were recognized, are based on color-banding unless the contrary is indicated.

Vocalizations of the Prairie Warbler are arbitrarily named and spelled with initial capitals. Names of other behaviors are not capitalized.

All times are eastern standard.

All dates are given in this order: day, month, year. In a few tables and lists, months are numbered rather than named; 4/5, for example, is 4 May.

Weather data.—Statements about weather are based on the United States Department of Commerce Weather Bureau's *Climatological Data*. Most Bloomington reports were by an Indiana University station located about 1 km from my study areas. In a few cases these reports were lacking and in a few others were clearly wrong in assigning rainfall to the wrong date. In such instances I used data from weather stations near Bloomington or made the necessary corrections.

Names of organisms.—Most organisms are referred to by vernacular names in the text. Appendix 8 gives the scientific names in such cases.

Determining sex and age of Prairie Warblers.—Beginning with Chapter 3, the question is often asked whether adult behavior varied according to sex and/or age. Age classes are yearlings or 1-year-olds on the one hand, older birds on the other. Readers having questions about sexing and aging methods and their reliability should consult Chapter 41, Appendix 5, and frontispiece. To summarize briefly, sexes were distinguishable by plumage, as were female age classes. Males classed as yearlings included some that were distinguishable by plumage, others that I banded as nestlings, and still others that occupied territories whose banded owners of the previous year had not returned and were believed dead (see p. 22 and Chapter 37). In this last group a few older males were probably included, because some old males abandoned former territories and moved (Chapter 5).

This is contribution number 1046 of the Indiana University Department of Zoology.

CHAPTER 1

HISTORY, PRESENT DISTRIBUTION, BREEDING HABITATS, POPULATION DENSITIES

INTRODUCTION

The Prairie Warbler (*Dendroica discolor*) is a common bird in various forest-edge habitats of the eastern United States and Canada. Its breeding range extends from the southern limits of the United States northward to roughly 45° N on a line from Maine to Michigan; west of Michigan it reaches much less far north (Fig. 4).

The mean monthly temperature in the northern part of the breeding range in the hottest month, July, is 21°C; in the south it is 27°C. Annual precipitation for the states bordering the Gulf of Mexico is occasionally as great as 150 cm; elsewhere in the range as little as 75 cm of moisture fall. Average relative humidity at noon in July in the eastern part of the range is 75%; this figure declines to 50% in the western part. (Data in this paragraph are from Kendeigh 1961: 293.)

Prairie Warblers breed under all extremes of substrate moisture, although a rather dry soil surface is typical for most populations. In the Appalachian Mountains the highest breeding elevation reported is at 1219 m above sea level in Virginia (Brooks 1940, J. J. Murray 1952: 95–96); but in most locations the species is found only at considerably lower altitudes (Bruner and Field 1912, Baerg 1927, Todd 1940: 532, Stupka 1963: 160, Mengel 1965: 419).

Two subspecies are recognized: *D. d. discolor* is a migratory form that breeds virtually throughout the range and winters in Florida and the West Indies; *D. d. paludicola* is a disjunct largely sedentary race that inhabits mangroves on the coasts of Florida. The Prairie Warbler is represented in the West Indies by a very similar species (Bond 1957), the Vitelline Warbler (*D. vitellina*), which occurs only in the Caymans and on Swan Island (Bond 1960: 200). Figure 4, a range map prepared from details supplied by local correspondents, shows the breeding distribution of the Prairie Warbler in the 1960's; see also Appendix 1.

The type specimen from which Louis Jean Pierre Vieillot described *Sylvia discolor* (1807, or 1808 or 1809 (date uncertain) :37; original not seen by me) is in the Royal Scottish Museum in Edinburgh. It does not retain its original label; details from that label are copied on the present one, but place and date of collection are not shown (I. H. J. Lyster pers. comm.). On 18 April 1810, Alexander Wilson found the species near Bowling Green in the "Barrens" of southwestern Kentucky, "prairie country . . . evidently resembling and perhaps representative of the tall-grass prairie" (Mengel 1965: 21). As a result of that experience Wilson gave the bird its vernacular name. The race *D. d. paludicola* was described by Arthur H. Howell (1930) from specimens collected in 1918 and thereafter. In a privately published paper dated "11-16-1926," H. H. Bailey (1926 or 1930; not seen by me) described the same form and named it *collinsi*, but Bailey's paper had had no public distribution at the time of Howell's publication (Van Tyne 1956). The A.O.U. Check-list (1957: 503) has therefore recognized Howell's description as having priority.

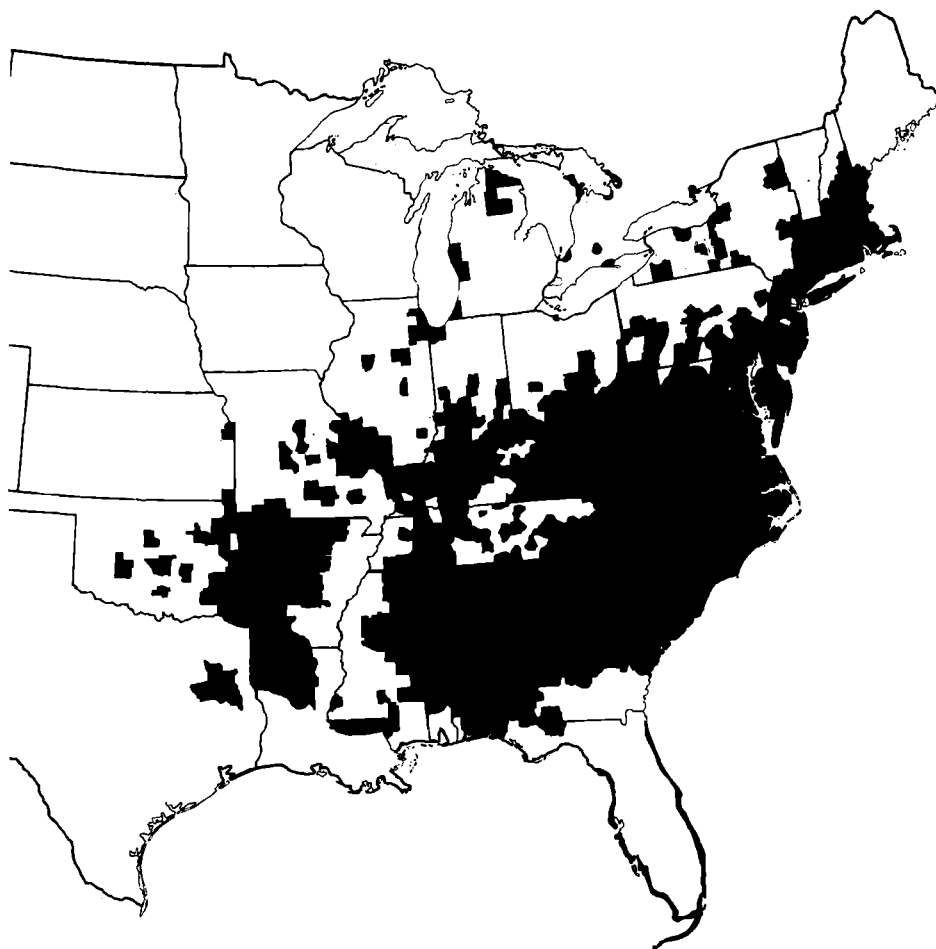


FIGURE 4. Known breeding range of the Prairie Warbler in about 1965. *D. d. paludicola* inhabits the shaded part of the Florida coast, *D. d. discolor* the remainder of the shaded area. For details, see Appendix 1.

At the time of its discovery the Prairie Warbler was probably a rare and local bird, with most populations scattered around the margins of its present range. Audubon (1967: 68) found it near Philadelphia and in "the Jerseys," among other places; but his account of its habits suggests that he did not know it well. Nuttall (1832: 294–296) described the breeding range as "the Atlantic states" and the two localities in which Wilson found it, i.e. Kentucky and the land of the Choctaw nation (Mississippi, to judge from Wilson's itinerary as described by Burns 1908). In 1860, New York was thought to be the northern limit of the range on the Atlantic coast (Baird, Cassin, and Lawrence 1860: 290; but see Brewster 1906: 346–347). The rarity of Prairie Warblers west of the Alleghenies in the 19th century is confirmed by Ridgway (1889: 156) and Wheaton (1882: 259–260). The only discovered exception to the conclusion that the species was "nowhere abundant" (Baird, Brewer, and Ridgway 1874: 276–279) is the report of August Gerhardt, who studied in northwest Georgia in the middle 1800's (Burleigh 1958:

8); Gerhardt considered the Prairie Warbler the commonest parulid in his area (Baird, Brewer, and Ridgway *loc. cit.*). One other early record is of particular interest: Abram Sager (1839) discovered the Prairie Warbler somewhere between Detroit, Saginaw Bay, and Jackson, Michigan (Wood 1951: 13). If there was a Michigan breeding population at this early date, it was probably disjunct.

To summarize, Cooke (1904: 96–97) was probably correct when he concluded as late as 1904 that the Prairie Warbler was “quite local in its distribution.”

EVOLUTION, EARLY DISTRIBUTION, RANGE EXPANSION

Kendeigh (1961: 298, 283) regards the Prairie Warbler's center of distribution as in the “south Atlantic and Gulf states . . . associated with the southeastern pine forest, the magnolia-oak forest, or with seral stages The evidence is inferential that [it] did not originally belong to the deciduous forest biome” and that it was a member of the old Madro-tertiary sclerophyllous woodland and pine forest (see also Mengel 1964: 30, 36). In the late Miocene or early Pliocene this plant community may have extended continuously around the north side of the Gulf of Mexico (Pitelka 1951: 383–384). Dispersal into and adaptation to forest-edge communities of the deciduous forest biome presumably took place during the Pleistocene.

The presence of *D. d. paludicola* on the coast of Florida has been variously accounted for (Norris 1951: 34, Robertson 1955: 434 *et seq.*). Perhaps most plausibly, Robertson points out that mangroves extended from Florida northward along the Atlantic coast during much of the early Tertiary and may have offered a forest-edge habitat near the range of the Prairie Warbler. A population could have invaded mangroves and then have followed them southward when they retreated to their present Florida location.

Prior to the arrival of European man in North America, shrub habitats and therefore Prairie Warbler populations were much less generally distributed than they are today. To gain some light on the probable distribution of the bird before settlement by Europeans, we may identify shrub communities that the Prairie Warbler inhabits today and that have probably existed for centuries in approximately their present locations, independent of human intervention. The following list indicates the character of such plant communities and their long-standing locations:

1. Open pine forests with a shrub understory.—The Carolinas (Shelford 1963: 87–88; Whitehead 1964, 1965, 1967); Oklahoma (Wilson 1963, George M. Sutton pers. comm.).

2. Rocky, unforested cliff edges and ridges including even “the smallest natural openings” in the mountain forests.—Kentucky (Mengel 1965: 81) and doubtless elsewhere in the Appalachians; also Arkansas where “virgin prairie-savanna” borders streams in the Ozarks (Douglas James pers. comm.).

3. Dry shrublands of the forest-grassland margin.—Eastern Kansas (Harrison B. Tordoff pers. comm., Goss 1891: 570–572), Arkansas (Douglas James pers. comm.), and Oklahoma. However, Kendeigh (pers. comm.) “very much doubt[s] if [the Prairie Warbler] was ever an important member of this community . . . in the contacts between grasslands and deciduous forest, here in the middle-west.”

4. Jack-pine plains.—Michigan (Mayfield 1960: Chapter 3).
5. Dunes.—Along Atlantic beaches in the United States and Lake Huron in Canada.
6. Mangroves.—Florida (Robertson 1955).
7. Miscellaneous unforested locations where edaphic factors have arrested succession, e.g. brushy zones along southern tidal streams.
8. Surprisingly, the closed forest of the Great Dismal Swamp today is inhabited by Prairie Warblers (Brooke Meanley pers. comm.) and therefore may have been from time immemorial.

In addition to these relatively stable, naturally occurring, potential breeding locations, habitats of short duration must have existed throughout the deciduous forest biome. These were probably occupied for a few years by Prairie Warblers and abandoned when the forest regenerated. Such habitats included sites of forest destruction by fire (Brown and Folweiler 1953; compare Griscom 1949: 60–61, 291–292; Griscom and Snyder 1955: 203–204), by insect outbreaks (Craighead and Miller 1949; compare Tyler 1919), and by disease (Gravatt and Parker 1949; compare Brooks 1940). Doubtless the Prairie Warbler also occupied brushland created by activities of the Indians. The extent and distribution of shrubland on vacated village sites, exhausted maize fields, areas exploited for firewood, and intentionally fired forest differed in various parts of the country (Bidwell and Falconer 1941: 8; Gray 1941: 6; Shelford 1963: 17, 56; Graber and Graber 1963: 502). Day (1953), reviewing the evidence from the northeast, concludes that the Indians modified the virgin forest considerably. Abandoned cultivated land often reverted to closed forest in as little as 20 years (Day 1953), but during much of that period the vegetation would have been inhabitable by the Prairie Warbler.

In sum, a range map with a line drawn to connect peripheral breeding populations of the Prairie Warbler at the time when European settlement began probably would differ little from an outline range map today. But within the periphery forests prevailed, and the species would have been largely absent. In the last two centuries or so it has filled in a great deal of this interior as man has destroyed most of the forests and as shrublands have become extensive. Human activities that have been responsible for the vast stretches of habitat now available to Prairie Warblers are farming, lumbering, strip mining, tree farming (especially the farming of Christmas trees and of pine trees in the southern states), and reforestation.

Agricultural practices favorable to the Prairie Warbler began very early. Fields were abandoned in Virginia in the 1600's because they had been exhausted by farming (Craven 1926: 32), and the cycle of clearing and soon abandoning land was repeated endlessly. By 1797, a traveler in Virginia and Maryland could write the following description of what is today a recognizable habitat of the Prairie Warbler: "Nothing is to be seen for miles together, but extensive plains . . . overgrown with yellow sedge and interspersed with groves of pine and cedar trees . . ." (Craven 1926: 58). Similarly, a census in Connecticut in 1796 showed that, in the four counties along the coast, between 29% and 39% of the land was "brush pasture," while in Massachusetts in 1801 "woodland and waste" accounted for 51% of Middlesex and Norfolk Counties (Bidwell and Falconer 1941: 119–120). Since the late 1800's the agricultural development most important in its impact on the

Prairie Warbler has been the shrinkage of farm acreage from its point of maximum expansion. The greatest part of the land taken out of farming has been abandoned to return to forest (John Fraser Hart pers. comm.). For example, Hart has calculated that the area of cleared farmland in New York in 1910 was 168% of the area in 1959. Such shrinkages can be restated as the creation of millions of hectares of shrubland in eastern North America.

Fires are probably commoner in areas altered by man than in pristine forest (Shelford 1963: 8), and forest fires have helped maintain areas of shrub habitat more extensive, and more long-lived, than would otherwise have been the case. The scale of some forest fires can be illustrated by the fact that a fire in 1952 burned 809,388 ha in Kentucky and West Virginia (U.S. Dept. Agr. Forest Serv. 1964: 30).

Except in the southeastern states, where the expansion of the Prairie Warbler population doubtless occurred too early to have been detected and recorded by observers, dates of colonization of newly available habitat can be documented to a considerable extent. (As evidence that populations in the southeast were already large in the late 1800's, there is Coues' 1888 statement that near Washington, D. C., he could find "perhaps more than fifty pairs" of Prairie Warblers, an "astounding" number for the small area he searched. See also Gerhardt's report from Georgia, pp. 7-8.) Observed changes in the status of Prairie Warblers include the following: establishment in the Connecticut River Valley probably about 1870 (Bagg and Eliot 1937: 567-570); extension into southern Ohio in about 1900 (compare Dawson and Jones 1903: 169-170; Henninger 1905, 1908; Hicks 1935: 172, 1936; Nolan 1958a), into southern Indiana in about 1910 (compare Butler 1897: 1076-1077, 1913, 1919, 1921; McAtee 1905), and into southern Illinois possibly at about the same time (compare Ridgway 1889: 155-157, Forbes 1908, Forbes and Gross 1923: 446, Graber and Graber 1963); invasion of Lake Michigan dunes of Indiana in 1909 (Coffin 1909, Stoddard 1916, Eifrig 1919) and of adjoining Berrien County, Michigan, in about 1917 (Wood 1922: 29); establishment in eastern Dutchess County, New York, between 1924 (Crosby, Frost, and Flewelling 1924) and 1936 (Preston 1936); "marked increase" into southeastern New York and northeastern New Jersey (Cruikshank 1942: 399, Fables 1955: 60) beginning in about 1935; extension to both slopes of the Allegheny Mountains in West Virginia (Brooks 1932, 1934, 1940) in 1927-1930, perhaps associated with lumbering of mountain forests; movement into western Pennsylvania probably in the 1950's (compare Todd 1940: 532-533, Harrison 1964, Parkes and Leberman 1963, Prager 1963); probable invasion of northern Louisiana west of the Mississippi River in about 1930 (Lowery 1931, Oberholser 1938: 548); "a great increase over the whole northeast" into New Hampshire and Maine between 1940 and 1948 (Griscom 1949: 292; see also Griscom and Snyder 1955: 203-204); penetration southward into interior Florida (by *D. d. discolor*) in about 1952 (Stevenson 1958, Gaither 1964); and extension into eastern Texas in the 1950's (Sheffield 1956).

Certain reports of the Prairie Warbler from locations in which it had been unknown probably represent discoveries of long established populations. Thus, although the species was not seen in Canada until 1900 (Samuel 1900, Ames 1901) and was not discovered nesting there until 1922 (in Simcoe County, Ontario; James

L. Baillie pers comm.), Jones (1910) in 1907 saw a great number of migrating Prairie Warblers on Cedar Point, Ohio, a sand spit projecting into Lake Erie toward Point Pelee, Ontario. And in 1910, the same author (Jones 1912: 102) reported that "almost unbelievable numbers" of Prairie Warblers and other warblers were found in migration on the islands of Lake Erie between Ohio and Ontario. Considering that the first known habitat in Ontario was stable, undisturbed dune vegetation (James L. Baillie, Jon Barlow pers. comm.) and that a breeding population may have existed for centuries or millenia in nearby Michigan (p. 8), the evidence points to long occupation of Ontario. Much the same may be true of Kansas (see Goss 1891: 570-572, Hedges 1953, Rising 1964).

PRESENT BREEDING ENVIRONMENTS

To the list (pp. 8-9) of communities that have long existed independently of human activity and that the Prairie Warbler inhabits today may be added the following habitats created by man's intervention: abandoned agricultural fields; unmowed apple orchards; strip-mined lands; Christmas tree farms and similar plantings; lumbered, burned, grazed forests and woodlands.

Appendix 2 gives details about the various breeding habitats, including their locations, structural and floristic characteristics, the approximate duration of the period in which each is suitable for occupancy by the Prairie Warbler, and some of the associated bird species. This information reveals that the nominate race is extremely versatile, occupying habitats ranging from very young communities in recently abandoned fields to mature woodland in the case of the Great Dismal Swamp. The preferred habitat is probably the one described by James (1971), who determined the basic life form of vegetation occupied by bird species breeding in Arkansas. Principal component analysis showed the Prairie Warbler as an "open-country bird . . . in places having high ground cover and few trees . . ." (*op. cit.* 225); no species among the 46 investigated exceeded the Prairie Warbler in occurrence in communities having those vegetational characteristics. James also used discriminant function analysis to reduce all measurements of vegetation structure to a single dimension and to locate bird species along "a continuum from xeric to mesic situations, from upland to bottomland, from low to high biomass, and from open country to forest associations" (*op. cit.*: 229-231). The Prairie Warbler was the terminal or extreme species at the xeric, upland, low-biomass, open-country end of the continuum (see also Shugart and James 1973).

It may promote understanding of Prairie Warbler habitat requirements and preferences to note where it is found when it occurs in association with other shrub-dwelling parulids. For this purpose I analyzed all breeding-bird censuses published in *Audubon Field Notes* (now *American Birds*) from 1947 through 1966. Where the Prairie Warbler and another wood warbler were reported as breeding on the same census plot I corresponded when possible with the census-taker and sought details. When Yellow Warblers and Prairie Warblers occur in proximity the Yellow is found in the more moist places, e.g. low ground bearing willows, or the less brushy places, e.g. yards and mowed orchards. (This is not true of the race *D. d. paludicola*, which often is found over water. Robert P. Allen, pers. comm., observed Yellow and Prairie Warblers on "adjacent territories" in mangroves, suggesting

territorial exclusiveness in that habitat.) Chestnut-sided and Prairie Warblers have extremely similar ecologies and are seldom sympatric; the Chestnut-sided is probably historically (Mengel 1964: 33 *et seq.*) and is certainly presently a more northern form. Where the two occur together in New England, their territories do not overlap; however, interspecific fighting has not been reported. On such tracts Chestnut-sideds tend to occupy cooler, moister, more deciduous, north-facing slopes; Prairie Warblers keep to the hotter, drier scrub, in which often there are pines as well as deciduous trees.

Pine and Prairie Warblers frequently coexist, the Pine foraging and nesting higher than the Prairie, preferring larger trees, and usually gleaning exclusively from conifers. Kirtland's Warbler and the Prairie Warbler occur together, but according to Mayfield (pers. comm.) their preferences are quite different. The Prairie "barely accepts prime Kirtland's habitat . . . [i.e.] nearly homogeneous stands of small pines." And whereas "the population density of Prairies increases where there is a generous admixture of deciduous shrubs, [this] condition . . . reduces the attractiveness . . . to the Kirtland's."

Common Yellowthroats and Yellow-breasted Chats often share habitats with the Prairie Warbler and did so on my study area. But both the former prefer the lower, denser, possibly more moist locations, and I rarely saw them forage in as high or as open situations as does the Prairie. The Blue-winged Warbler also frequently occurs with the Prairie Warbler and did so on my study area, but the Prairie invades abandoned fields several years earlier than the Blue-wing. Clearly the Blue-wing prefers denser growth, as would be expected from the frequency with which it feeds by probing the buds of trees (Robert Ficken, paper read at 1965 meeting of the American Ornithologists' Union).

POPULATION DENSITIES

Methods.—Table 1 presents Prairie Warbler population densities and selected details from censuses, most of which appeared in *Audubon Field Notes* and *American Birds*. Omitted are censuses covering very heterogeneous habitats and certain habitats that were obviously marginal for Prairie Warblers. In the few censuses taken over more than one year, I combined data from as many years as possible and averaged them. I selected fewer than all the years if the investigator relocated the boundaries of his tract, or if the vegetation had been cut or sprayed between census years, or if plant succession had so changed the tract that averaging would be meaningless.

The population density in the Lake Michigan dunes is based on censuses by Holly Reed Bennett (pers. comm.). I later inspected and measured his census area and calculated population density from my measurements.

It should be noted that censuses made in only one year may reflect short-term deviations from normal densities. Further, censused areas were small, many no more than 6 ha; sampling errors and effects of variation in field work may have been greatly magnified by extrapolation to pairs per 40 ha, the standardized form in which densities were published.

Results; discussion.—Inspection of Table 1 suggests several tentative conclusions:

TABLE 1
DENSITY¹ OF PRAIRIE WARBLER IN VARIOUS HABITATS, ACCORDING TO DOMINANT VEGETATION

Census number	Description of habitat	Location	Pairs per 40 ha ²		Number of spp.	Number of spp. more numerous than Prairie Warbler ³	Source
			Prairie Warbler	All spp.			
Dune							
1	Lake Michigan dunes	Ind.	60	—	—	—	Calculated from pers. comm. from H. R. Bennett
Mangrove							
2	Mangroves	Fla.	9	55+	14	2 ⁴	Robertson 1955: 424
Mixed pine, deciduous							
3	Slash-longleaf forest	Ga.	2	50	13	4	Aldrich and Burleigh 1946
4	Jack-pine plains	Mich.	12.5	158	12.5	1	Van Tyne <i>et al.</i> 1942, 1943
5	Shrub pine, 20 years old	Ga.	6	127	13	6	Johnston and Odum 1956
6	Young forest, 25 years old	Ga.	6	83	10	4	Johnston and Odum 1956
7	Piedmont pine-oak forest, 1–10 years old	N.C.	17	249	31	5	Oelke 1966a
8	Piedmont pine-oak forest, 10–20 years old	N.C.	18	179	21	4	Oelke 1966b
9	Pine-oak, barren	N.J.	13–19 ⁵	126	*	1	Fables 1947, 1948, 1949
10	Abandoned pasture, mostly cedars	W.Va.	23	167	17	1	Hall 1955
11	Abandoned field	W.Va.	37	167	9	0	Laitsch <i>et al.</i> 1957
12a	Densely overgrown field, mean tree height 4 m	N.C.	47	225	17	0	LeGrand and LeGrand 1967
12b	Same, 3 years later; sapling-brushland	N.C.	53	247	18	0	LeGrand 1970
13a	Power right-of-way 7 years after clearing	Md.	80	388	14	0	Longcore 1971
13b	Same, 8–9 years after clearing and after removal of larger interfering trees	Md.	52.5	375	15.5	0	Longcore 1971
14	Thick oak scrub with few pines	Mass.–R.I.	29	*	*	*	Childs 1964 and pers. comm.
15	Abandoned, pine-planted field	Pa.	44	378	24	1	Prager 1963
16	Immature Loblolly-Shortleaf Pine	Md.	48	347	27	1	Springer and Stewart 1948
Deciduous							
17	Oak scrub, after fire	Mich.	14	242	25	2	Walkinshaw <i>et al.</i> 1944
18	Abandoned field	Ind.	19	?	18	5 or 6	This study
19	Abandoned field, dense shrubs	Ind.	23	?	17	5 or 6	This study
20	Abandoned field	Ohio	28	194	9	2	Aldrich and Moulthrop 1939
21	Pasture-thicket	Conn.	11	287	32	4	Goodwin and Goodwin 1964
22	Abandoned pasture	Conn.	20	315	15	5	Rayfield <i>et al.</i> 1961
23	Upland brushy pasture	Conn.	34	287	27.5	1	Magee and Enders 1965, Magee and Cavanaugh 1966

TABLE 1. Continued

Census number	Description of habitat	Location	Pairs per 40 ha ²		Number of spp.	Number of spp. more numerous than Prairie Warbler ³	Source
			Prairie Warbler	All spp.			
24	Brushy hilltop	W.Va.	33	307	25	2	Anderson <i>et al.</i> 1970
25	Lumbered oak forest	W.Va.	23	180	20	0	Harrison <i>et al.</i> 1962
26	Field abandoned 5-15 years	Ky.	37	*	*	3	Stamm <i>et al.</i> 1958, much modified by pers. comm.
27	Field abandoned 10 years	Md.	54	*	9 probably	0	Warbach 1958
28	Moist scrub, after fire	Md.	50	331	37	2	Stewart <i>et al.</i> 1947
29	Dry scrub, after fire	Md.	85	288	28	0	Robbins <i>et al.</i> 1947
Apple orchard							
30	Unmowed	Md.	18	234	14	3	Springer and Stewart 1948
31	Unmowed, but sprayed	W.Va.	7	160	24	5	DeGarmo 1949
32a	Infrequently mowed, May	Md.	2	91	12	3	Springer and Stewart 1948
32b	Same, June of same year, no further mowing	Md.	18	177	18	3	Springer and Stewart 1948

* Omitted because unknown or because internal evidence shows datum to be useless.

¹ Censuses 4, 9, 13b, 17, 18, 19, and 25 were taken in more than 1 year; for each, the annual results are averaged. See text.

² Areas of census plots differed and in most cases were much smaller than 40 ha. Densities shown were obtained by extrapolating to 40 ha.

³ Where the census covered more than 1 year, the number of species breeding is the mean. A species' rank in abundance is based on the average.

⁴ Redwinged Blackbird and Least Tern were more abundant.

⁵ Published data are not clear but probably mean that density was 19 rather than 13 pairs per 40 ha.

1. Population densities in entirely deciduous and in mixed pine-deciduous communities do not appear to differ.

2. Population density seems positively correlated with biomass of green vegetation above the ground level and especially with density of the shrub layer, provided there is no closed canopy. The common characteristic of all tracts (except census 1 and possibly census 23) in which there were more than 30 pairs per 40 ha was abundant foliage widely distributed on twigs and small branches considerably exposed to sun. Census 6 is a partial exception; the trees were 10–28 m high and were nearing the stage of closed forest.

Certain pairs of plots suggest that between two tracts in the same general location the shrubbier, leafier tract had the larger Prairie Warbler population: Fables (1939) reported that Prairie Warblers were denser in the burned, more overgrown part (1938) of his study area (census 9) than in the unburned part. The West Virginia tract (census 11) that held 37 pairs per 40 ha was 75% covered with low trees and shrubs, whereas the West Virginia tract (census 10) with 23 pairs per 40 ha was only 40% covered. The shrubbier parts of my study area held more territories than did the parts grown up largely in broom-sedge and those in which recent mowing had reduced the shrub layer. Censuses 12a and 12b covered the same plot in different years; censuses 13a and 13b did approximately the same. In each case Prairie Warbler density was higher when the indications are that there was more foliage.

3. The preceding paragraph may suggest that population density was correlated at least in part with insect abundance. A similar indication is the low density in mangroves, with their often bare or inundated substrate, and in cultivated orchards. An orchard (censuses 32a and 32b) that held 2 pairs per 40 ha just after having been mowed held 18 pairs later in the same summer after a thick grass and herbaceous cover had grown up. After this increase in vegetation, this orchard was as densely populated as one that had been left unmowed (census 30). The possible relevance of the difference in density between sprayed and unsprayed orchards (censuses 30 and 31, respectively) is obvious.

4. The high density in the sparse scrub of the Indiana dunes may be attributable to the ribbon-like configuration of territories. Suthers (1960) found that Song Sparrow territories along a lake were quite small, intermediate between those of inland habitats and the sometimes tiny territories of little islands (see p. 332). Further, few other bird species occur in the dunes, and the competition for insects must be slight. This, however, is also true of mangroves.

5. Xeric communities appear to hold higher densities of Prairie Warblers than do mesic. The Maryland censuses 28 and 29 show a substantial difference between counts on a damp scrubby area and a nearby dry one. The vegetation on the two plots was of identical age, consisting of reproduction after the same forest fire.

6. Numbers of Prairie Warblers per tract and size of the total bird population are closely and positively correlated.

7. Prairie Warblers appear to be unusually dense in Maryland and possibly Virginia and North Carolina, i.e. in the region in which the species has probably inhabited extensive areas for two or three centuries (see p. 9). Censuses 29 and 13a report by far the highest densities that I know, and census 16 shows a remarkably high figure considering that the trees were approaching the forest stage.

The greatest density in any abandoned field (census 27) was in Maryland; see also the data in Stewart and Robbins (1958: 299). Further, occurrence of the Prairie Warbler in tended Maryland apple orchards, probably a very marginal habitat, points to considerable population pressure there. That the same orchard (censuses 32a and 32b) held fewer territories in mid-May than it did a month later is surprising; the number of breeding individuals would more likely have been expected to decrease between May and June (see Chapter 31). This invasion of the orchard in midseason may indicate the existence in Maryland of a floating population, ready to move into newly available areas. Finally, Meanley's discovery of territorial Prairie Warblers in the mature forests of the Great Dismal Swamp, in association with such moisture-loving species as Prothonotary Warblers (see Appendix 2), may point to the occupation of a most unusual habitat as the result of population pressure.

CHAPTER 2

THE PRAIRIE WARBLER IN WINTER

DISTRIBUTION AND HABITATS

The A.O.U. Check-list (1957: 502–503) considers the winter range of *D. d. discolor* to lie entirely in the West Indies and certain islands off Central America, whereas Bond (1956: 151–152) regards Florida as also within the winter range. Museum collections do contain a few specimens referred to as *discolor* and collected in Florida in winter (e.g. USNM 102374, USNM-BS 342924, CNHM FM94860), but the significance of this is not clear; accidental occurrences of Prairie Warblers in various states in winter are rather numerous (see Chapter 36). Certainly the bulk of *discolor* winters in the West Indies, where Bond (1956: 152) says that it is common in the Bahamas and Greater Antilles and not uncommon on the more northern of the Lesser Antilles, as far south as Martinique. Off the coast of Central America, it is found from Isla Mujeres at about 22° N to Great Corn Island at about 12° N.

The race *paludicola* winters principally in Florida, but individuals have been recorded in Cuba and on St. Croix in the Virgin Islands (Bond 1956: 152, A.O.U. Check-list 1957: 503).

All breeding habitats of the Prairie Warbler appear to have their structural counterparts in winter habitats. Perhaps more frequently than in the breeding range, the bird occupies forests on some islands. The great increase of Prairie Warblers in recent decades presumably has affected the population density in the winter range and may have led to occupancy of a wider range of plant communities. Appendix 3 presents available details on winter habitats, listed geographically. The sources from which the information is taken do not distinguish between races, but almost certainly the references are to *discolor*.

BEHAVIOR

The following information, which was taken from the literature, probably pertains to the race *discolor*, except for the statements about the beginning of song in *paludicola*.

In Cuban woods Eaton (1953) found Prairie Warblers joining other winter-resident wood warblers and endemic species in loose flocks whose members tended to forage at preferred, species-specific heights. Regular members of these aggregations were Black-and-white Warblers, Northern Parula Warblers, Black-throated Blue Warblers, and American Redstarts. These and Prairie Warblers were represented by two to five individuals per flock. Prairie Warblers often associate with Palm Warblers in and near Nassau, Bahamas, during winter (Robert W. Hanlon pers. comm.).

Whether the individual Prairie Warbler stays in one home range all winter is unknown, but at least some individuals probably do. Robert W. Hanlon (pers.

comm.) and Brother Ignatius Dean banded a Prairie Warbler (USFWS 29-03518) of unknown sex at Nassau, Bahamas, on 6 March 1959, and netted it again there on 10 September 1959. Conceivably this bird was migrating past the point on both occasions, but much more probably it was on its winter location. Walkinshaw and Baker (1946) observed a single individual daily at Santa Barbara, Cuba, from 15 to 24 March. Other parulids show fidelity to winter home ranges (Snow and Snow 1960, Schwartz 1963, Nickell 1968, Ely 1973).

Eaton (1953) states that the foraging zone in Cuban woods is the "tops and central areas of the trees." Lack and Lack (1972) accumulated considerable numerical data on the ecology of the 20 parulids that winter on Jamaica; their analysis of Prairie Warbler foraging coincides with my observations in Indiana (Chapter 39).

Alexander Wetmore (pers. comm.) states that the Prairie Warbler does not sing in midwinter in the West Indies, and the literature mentions no winter singing. Some males start to sing in late March, however, just before migrating or possibly after migration has actually begun (Peters 1917: 420, Wetmore and Lincoln 1933: 56). Individuals wintering in Florida, probably *paludicola*, are silent until about the end of January, then begin to sing (Robert P. Allen pers. comm., William B. Robertson pers. comm.).

CONDITION PRECEDING SPRING MIGRATION

Prenuptial molt occurs in most Prairie Warblers between January and March (Chapter 41), but Nolan and Mumford (1965) found molt still in progress in 23% of the males and 6% of the females that were killed by striking a television tower during spring migration through northern Florida.

Fat is evidently deposited before the northward movement begins (compare D. W. Johnston 1968). Wetmore and Lincoln (1933: 56) speak of "excessively fat" birds gathering for migration, and Wetmore (1927: 519) tells of collecting a very fat migrant on 6 April in Puerto Rico. Danforth (1925: 121) reports two such experiences. Walkinshaw (reported in Nolan and Mumford 1965) obtained weights from 10 Prairie Warblers caught on Andros Island, Bahamas, between 18 and 25 March. The mean was 7.5 g, the extremes 5.9 g and 8.2 g. Judging from weights prior to overwater migration in autumn (Chapter 36), the weights recorded by Walkinshaw may represent the winter lean condition (see also Appendix 7).

Just preceding, or as the first noticeable stage of, spring migration, Prairie Warblers may become increasingly gregarious. Wetmore and Lincoln (1933: 56) speak of their "evidently gathering for migration" in the mesquite of Terrier Rouge on Hispaniola in late March.

CHAPTER 3

SPRING MIGRATION

DATES

Departure from winter range.—Dates of earliest occurrence of Prairie Warblers just beyond the winter range imply that the first migrants probably leave winter quarters about 1 March. Thus, 200 Prairie Warblers were observed at Sombrero Key in southern Florida on 3 March 1889 (A. H. Howell 1932: 410). Also on 3 March, Bent and Copeland (1927) saw a supposed migrant near St. Petersburg, Florida, and the earliest death resulting from collision at a television tower near Tallahassee is 15–16 March (Stoddard 1962: 73). A Prairie Warbler was found on the Gulf coast of Alabama on 3 March (Imhof 1962: 476) and another on Dauphin Island on 11 March (Thomas A. Imhof pers. comm.).

Cooke (1904: 98) was probably correct that the “full tide of migration . . . does not start until the last of March.” This is suggested by a frequency distribution (Table 2) of dates of death of Prairie Warblers that collided with television towers near Tallahassee, Florida, at the southern edge of the breeding range of *discolor* (Nolan and Mumford 1965; see also the analysis below of the migration schedules of the sex-age classes). Although the magnitude of migration is not necessarily correlated with numbers of collisions (see Nolan and Mumford 1965), it is probably significant that the heaviest fatalities are in April (see Table 2). Numbers of Prairie Warblers in the West Indies decline in April (Northrop 1891, Todd 1916: 265), and the last migrants evidently leave the winter range in May. Some late dates are these: Hispaniola, 22 April (Wetmore and Swales 1931: 386); Puerto Rico, 22 and 23 April (Danforth 1931: 94); Nassau, Bahamas, 7 May (Robert W. Hanlon pers. comm.); Sombrero Key, Florida, 11 May (collided with lighthouse; A. H. Howell 1932: 407); Cay Lobos, north of Cuba, 13 May (collided with lighthouse; Bonhote 1903); unstated location in West Indies, 13 May (Bond 1964). Stoddard’s (1962: 73) latest record of a casualty at the television towers near Tallahassee was 16 May (Stoddard and Norris 1967: 21).

Arrival in breeding range.—Dates of arrival at various points in the breeding range are given below. Earliest dates are shown; averages were rejected, following Stevenson (1957: 45–46). Omitted are records so late that they obviously reflect deficient information and February dates, which probably apply to overwintering birds.

Georgia—Savannah, 8/3; Atlanta, 26/3 (Burleigh 1958: 539). Alabama—lower coastal plain, 3–11/3 (Imhof pers. comm.); Birmingham, 30/3 (Imhof 1962: 476); Tennessee Valley, 2/4 (Imhof pers. comm.). Mississippi—Gulfport, 6/4 (Bent 1953: 437); Pearl River Co., 3/4 (B. E. Gandy pers. comm.). Louisiana—Baton Rouge, 25/3 (Lowery 1960: 521); Monroe, 30/3 (Oberholser 1938: 548). South Carolina—coast (probably), 21/3 (Wayne 1910: 171–172); Piedmont, 11/4 (Sprunt and Chamberlain 1949: 469). North Carolina—Wilmington, 20/3; Raleigh, 5/4 (Pearson *et al.* 1959: 329). Virginia—

TABLE 2
DATES¹ OF DEATH OF 211 SPRING MIGRANT PRAIRIE WARBLERS NEAR
TALLAHASSEE, FLORIDA, ACCORDING TO SEX AND AGE

Dates	Males				Females				Totals
	Old ²		Yearling		Old		Yearling		
	N	%	N	%	N	%	N	%	
19-31 March	22	76	2	7	4	14	1	3	29
1-10 April	36	80	0	0	7	16	2	4	45
11-20 April	27	39	10	14	26	38	6	9	69
21-30 April	9	14	6	10	35	56	13	21	63
1-13 May	2	40	1	20	0	0	2	40	5
Totals	96		19		72		24		211

¹ All birds are treated as having died after midnight.

² These showed no immature plumage but probably include some yearlings; see Chapter 41 and Appendix 5 where methods of aging are discussed.

location not stated, 2/4 (J. J. Murray 1952: 95-96); second week of April, location not stated (Bailey 1913: 302). Tennessee—Knox Co., 5/4 (Howell and Monroe 1957: 301); Cades Cove, 3/4 (Stupka 1963: 159). Arkansas—Fayetteville, 5/4 (Baerg 1931: 144). Oklahoma—location not stated, 16/4 (Sutton 1967: 511). Maryland and District of Columbia—District of Columbia, 12-15/4; Anne Arundel Co., 12/4 (Stewart and Robbins 1958: 298-299). Kentucky—Warren Co., 6/4; many locations, 12-13/4 (Mengel 1965: 418). Missouri—St. Louis, 11/4 (Bent 1953: 437). New Jersey—Cape May, 30/4 (Stone 1937: 830). New York—New York City region, 16/4 (Bull 1964: 386); Buffalo region, 2/5 (Beardslee and Mitchell 1965: 385). Pennsylvania—location not stated, 16/4 (Poole 1964: 57). Ohio—Fremont, 11/4 (Bent 1953: 437); central Ohio, 16/4 (Borror 1950: 26); Cleveland region, 12/4 (A. B. Williams 1950: 138). Indiana—Bloomington, 11/4 (this study). Illinois—Chicago region, 6/5 (Ford *et al.* 1934: 63). Kansas—Lake Quivira, 28/4 (Bent 1953: 437). Connecticut—Portland, 27/4; New Haven, 27/4 (Sage *et al.* 1913: 159). Massachusetts—West Roxbury, 29/4 (Griscom and Snyder 1955: 204); Cape Cod, 1/5 (Hill 1965: 261); Connecticut River Valley, 1/5 (Bagg and Eliot 1937: 567). Michigan—Berrien Co., 12/5; Ann Arbor, 2/5; Huron Co., 7/5 (Wood 1951: 404-405). Ontario—Toronto, 17/4 (Bent 1953: 437).

Duration of arrival period.—A few examples suggest this period's duration. At Bloomington in a year in which the first Prairie Warbler appeared on 15 April, I found a male singing among a mixed flock of migrant warblers in a city yard on 24 May. In a year in which the first female appeared on 22 April, a young female that had not yet nested (she lacked an incubation patch) appeared on the study area about 1 June. In Maryland and the District of Columbia, Stewart and Robbins (1958: 298-299) report extreme arrival dates as 15 April and 25 May. In New York City and its vicinity, where the first pronounced wave is usually seen in early May, a few migrants are still found in the last week of May and occasional birds may arrive in June (Cruickshank 1942: 400, Bull 1964: 386).

Migration schedules, according to sex and age.—Data from Florida show that at the southern edge of the breeding range males appear earlier on the average than females. Males also arrive on their breeding grounds at Bloomington before fe-

males. Data also strongly suggest that yearlings tend to migrate later than older birds. Birds were aged as yearlings or older, using plumage characters described in Appendix 5 unless the contrary is stated. The old-bird class of males will include some undetected yearlings when plumage is the basis for aging, for reasons given in Chapter 41.

Florida data: Russell Mumford and I obtained data on plumage and gonads of 211 spring migrant Prairie Warblers killed in nocturnal collisions with towers near Tallahassee. This sample included all birds of this species found by Herbert L. Stoddard in spring, from 1958 through 1968, except some decomposed or mangled specimens. Collisions were arbitrarily assumed to have occurred after midnight. Other details of methods and problems are described in Nolan and Mumford (1965). Mumford and I make the assumptions that (1) Prairie Warblers killed were random samples of the migrants of that species at the times and place of death, at or below tower heights and (2) pooling of data from all years does not distort results.

The median date of death of the full sample of 211 was 16.6 April, of 96 old males 6 April, of 72 old females 20 April, of 19 yearling males 18 April, of 24 yearling females 26 April. Table 2 gives additional details and shows deaths according to 10-day intervals. Median tests of the data were performed. Dates of death of old and yearling males differed significantly (adj. Chi-square = 12.6; $df = 1$; $P < 0.001$), but old and yearling female dates did not differ. Old male dates were earlier than those of old females (adj. Chi-square = 38.6; $df = 1$; $P < 0.001$), but dates for yearling males and yearling females did not differ.

Nights of heavy mortality were nearly twice as numerous in April as in March and over four times as numerous in April as in May (Stoddard 1962: 19). Therefore differences in schedules of sex-age classes may be greater than the samples reveal. Heavy mortality in May would probably have yielded a high proportion of young birds, especially of females.

Indiana data: The mean date of first arrival of males on my study area, 1952 through 1967, was 18.6 April (extremes, 11 and 27 April). First females arrived on the mean date 23.4 April (extremes, 19 and 28 April). The earliest female never preceded the earliest male. The mean interval separating first male and female in the same year was 5.1 days (extremes, 1 and 9 days). I probably saw birds on the day they returned; even while migrating, males are conspicuous by their song, and territorial behavior begins immediately upon arrival. Females in turn attract territorial males, whose behavior indicates that a female is present.

More representative of the arrival time of the population of each sex are dates on which the fifth male and the fifth female appeared; the number 5 corresponds roughly to the median of known arrival dates of residents. During 12 years, dates for the fifth male ranged from 16 April to 28 April (mean, 21 April). For the fifth female extreme dates were 24 April and 1 May (mean, 28 April). Males were always earlier; the smallest difference between male and female dates in any year was 3 days, the greatest 10.

In the 2 years in which the difference in male and female dates was only 3 days, the dates for the fifth male were 25 and 28 April; in the 2 years in which the difference was 10 days, the dates for the fifth male were much earlier, 18 April in both cases. That is, when male migration was late females were not similarly late.

First arrivals tended to be old birds. In 10 different years, banded males known to be old returned to the study area; in 8 of the 10, one or more of these birds arrived on the first day on which Prairie Warblers were seen. In the other two years, banded males returned on the second day. Usually the first two or three males seen each year were banded.

Similar results come from a comparison of arrival dates of 32 males thought to be yearlings and 61 banded old males. Five of the yearlings were aged by their plumage (Appendix 5). The other 27 occupied territories of banded males that had failed to return and therefore can probably be presumed dead (Chapter 37); these 27 may include a few old males that had abandoned territories elsewhere and relocated to the study area (Chapter 5). A male was counted as 1 for each year it supplied a date. Because the data from both samples are taken from several years, relative arrival dates are used. In each year the day the first male or males arrived is day 1, the following day is day 2, etc. The two samples were distributed among the years in about the same proportions. The median relative arrival day of the old males was day 4; that of the males assumed to have been young was day 8; the common median was day 5; in the median test, adj. Chi-square = 11.3; $df = 1$; $P < 0.001$.

It also seems clear that first-year females tend to arrive somewhat later than old birds. Female age classes can be reliably detected by inspection of plumage (Chapter 41), and in 10 years I recorded the ages of the first five females that appeared on the study area. Of these, 46 females were old and 4 were yearlings. The ratio of old females to yearlings in the population was 2:1 (Chapter 38), and the significance of the 46:4 ratio is obvious. Despite the rarity of returns by banded females (Chapter 37), the first females seen, 1959–1964, were banded and old. Similarly, in three instances of unusually late pair formation by females known to be laying their first eggs of the season (they lacked incubation patches when they began to nest), two had been banded as nestlings in the preceding year and one was recognizable as a yearling.

MIGRATION ROUTES

Positions of Prairie Warblers found dead or observed in flight in spring between the West Indies and the mainland of the United States were as follows:

Dry Tortugas; 24° 40' N, 82° 50' W (Bent 1953: 438)
Sombbrero Key; 24° 37' N, 81° 06' W (A. H. Howell 1932: 410)
Cay Lobos; 22° 27' N, 77° 35' W (Bonhote 1903)
at sea near 23° 58' N, 81° 20' W (Hill 1957)

Considerable evidence suggests that some individuals move directly northwestward across the Gulf of Mexico instead of flying first toward Florida and then northward along that peninsula. After analysis of comparative abundance of Prairie Warblers at various points and of sequences of arrival dates, Stevenson (1957: 55, 65, 73) concluded that a flight up the Florida peninsula is clearly indicated but that a transgulf migration to Alabama and other locations probably occurs as well. Stoddard (1962: 14, 16, 18) presents evidence from northern Florida suggesting a transgulf migration (see also Lowery 1960: 443).

If some Prairie Warblers undertake direct migration across the Gulf, others may make a similar overwater flight on the Atlantic side of Florida. Many "precipitate on the southern Atlantic coast" (Stevenson 1957: 73). The earliest dates of arrival in Georgia, South Carolina, and North Carolina are at coastal locations, whatever the routes by which they are reached, with later dates recorded inland. The coast of Virginia may also be reached before inland stations.

ORDER IN WHICH BREEDING RANGE IS REOCCUPIED

It is probable that at least some of the earliest arrivals in the southern parts of the breeding range remain there to nest and that sections of the range are re-occupied by breeding populations at progressively later dates the more remote they are from the West Indies. Evidence for this is twofold: (1) Most of the earliest males seen each year at Bloomington remained there and bred, as revealed by banding and by my recognition of many unbanded individuals by song (Chapter 8), appearance, and continuity of behavior from day to day. A weakness in the value of this evidence may be that Bloomington's location is so far toward the periphery of the breeding range that few migrants pass through it toward more remote destinations. (2) There seems to be a rough positive correlation between arrival dates and nesting dates at various latitudes in the few cases in which these are known. Examples of earliest arrival dates followed by earliest egg dates for the same states are these: Georgia, 8 March, 22 April (Burleigh 1958: 539-540); Indiana, 11 April, 2 May (this study); Michigan, 2 May, 26 May (Walkinshaw 1959). The simplest and most probable interpretation is that the populations that nest first also have arrived earlier and that the breeding range is settled approximately from south to north.

BEHAVIOR DURING MIGRATION

The many nocturnal collisions near Tallahassee establish that much migration is at night. The heights of the original tower and of its successor (205 and 308 m) suggest the maximum heights at which the birds killed were flying, although the migrants may have been attracted to the towers and descended. Mumford and I detected no differences in the sex-age composition of the Prairie Warblers killed by the two towers.

Diurnal migration also occurs. Wetmore (1916b) found Prairie Warblers moving always to the westward on Vieques Island, Puerto Rico, between 19 and 27 March, a "marked diurnal movement" (1927: 519). He witnessed another such migration in Puerto Rico on Culebra Island on 9 April (1916a: 102). Hill (1957) reported migration of an estimated 1800 warblers, including Prairie Warblers, and of larger birds "passing from the Bahamas and the eastern half of Cuba to Florida" on 6 May 1955, beginning at about 1300 and continuing into the night. Groups of 5-15 birds passed Hill's ship, the majority flying "about fifty feet above the water, but some flocks . . . just above the waves and some at an estimated two hundred feet." A number of birds including 12 Prairie Warblers alighted on the ship. Because the weather was mild and "essentially normal," Hill concluded that the flight was "a part of the normal spring migration."

It is not known whether Prairie Warblers migrate singly at night or in flocks. Migrants during the day in the West Indies are seen both singly and in small groups (Wetmore 1916b), in association with other species of parulids (Wetmore 1916a: 102). Hill's (1957) description of flocks of warblers has just been mentioned; the composition of flocks is not stated, but eight species of wood warblers in addition to Prairie Warblers came aboard the ship.

Males begin to sing while in the West Indies (Chapter 2), and migrants continue to do so as they pass northward. I have four observations of prolonged singing in April by males that the circumstances indicated were migrating. All sang irregularly; the mean rate was about one song per min. Most songs lacked vigor and volume and seemed to be shorter than songs of territorial males. In contrast to territorial males in early spring, these probable migrants varied their songs considerably among song groups and versions (see Chapter 8 for this terminology).

MISCELLANEOUS DATA

Influence of barometric pressure systems on spring migration of many eastern North American species is reasonably well understood (see Pettingill 1970: 270–271). Arrival dates of Prairie Warblers in southern Indiana show that these birds responded typically to such weather systems. For example, the first birds of the year invariably returned on southerly winds, and the passage of a cold front or the dominance of a stationary high pressure cell interrupted this early flight of Prairie Warblers. Comparison of the annual first arrival dates in Chapter 4 with weather information published in *Audubon Field Notes* (now *American Birds*) will reveal many such correlations.

Weights, fat classes, and molt conditions of migrants killed during nocturnal migration near Tallahassee, Florida, have been analyzed elsewhere (Nolan and Mumford 1965). Approximate measurements of the gonads of 156 specimens were recorded. In males extremes of testis size along the long axis were 1 and 6 mm (mean, 3.5 mm). Males showing yearling plumage may have had slightly smaller testes on the average. There was no apparent correlation between size of testes and date of death. The ovaries of females were 2–7 mm × 2–4 mm; the mean long measurement was 3.5 mm. Ovaries of yearling females probably averaged slightly smaller than those of old birds. Variations in size appeared unrelated to date.

CHAPTER 4

REPOPULATION OF THE STUDY AREA IN SPRING

THE STUDY AREA AT TIME OF PRAIRIE WARBLER'S ARRIVAL

Vegetation.—The mean date of arrival of the first Prairie Warbler on the study area ("arrival day") for the years 1952–1967 was 19 April. Despite considerable annual variation in early spring weather, which was responsible for a difference of 15–20 days in the dates at which trees began to leaf out in April, in all years the general aspect of the vegetation on arrival day remained much as in midwinter (see Fig. 5). Close inspection revealed that some of the commonest woody plants had small leaves or were in flower. The estimated times, in days before (–) or after (+) arrival day, at which 30–50% of the population of prominent woody plants acquired small leaves (or flowers when that is specified) follow: American Elm –1, Black Cherry –6, Tulip Poplar –3, Sugar Maple +5, Sugar Maple (flowering) –4, Redbud (flowering) 0, *Rubus* spp. –5. These estimates are means for 7 years.

Many grasses and forbs began visible annual growth at about the same time as the plants above, and most other conspicuous vegetation of the study area did so soon afterward. Between 4 and 13 days after arrival day, depending on the year, the landscape presented a light green appearance. A summer aspect usually was assumed within another week or two.

Vertebrates.—Most bird species that had been present before arrival day were primarily granivorous at that season; examples are Bobwhite, Common Crow, Brown-headed Cowbird, Cardinal, American Goldfinch, Rufous-sided Towhee, and Field Sparrow. A few sedentary and early-migrant carnivores were also present, foraging in woods and in tree rows at the edges of the shrubland and relying on specialized feeding behavior or food, e.g. bark feeding or probing for earthworms, for their animal food. Among these were American Woodcock, various woodpeckers, Carolina Chickadee, Tufted Titmouse, and Brown Thrasher.

Closely associated with arrival day was the return of many breeding insectivores. The list that follows gives the time of first arrival (mean of 8 years) of selected species that bred in or adjacent to Prairie Warbler habitat, in days before (–) or after (+) arrival day: House Wren 0, Gray Catbird +6, Wood Thrush +2, Blue-gray Gnatcatcher –13, White-eyed Vireo +2, Red-eyed Vireo +6, Blue-winged Warbler +5, Common Yellowthroat +5, Yellow-breasted Chat +3, Scarlet Tanager +4, Summer Tanager +5, Indigo Bunting +9. Data for a few other insectivores are less complete. Whip-poor-wills preceded the Prairie Warbler by about 2 weeks, and Yellow-billed and Black-billed Cuckoos usually followed the warbler by at least 2–3 weeks. It is interesting that the Prairie Warbler arrived slightly earlier than most of the other insectivores.

The common reptiles emerged within a period that coincided with the return of most insectivorous birds. The mean times (5–8 years) for first sightings of sev-



FIGURE 5. Usual appearance of vegetation at the time the first Prairie Warblers arrived in spring. Photograph of part of Griffey Tract, 18 April 1958, by Gerald N. Svetanoff.

eral species, again in days before or after arrival day, follow: Box Turtle +3, Eastern Fence Lizard -11, Rough Green Snake +4, Racer +1, Rat Snake +5.

Arthropods (food).—Insects and arachnids had emerged before the arrival of the insectivorous birds, but efforts to collect them suggested that they were still far below summer numbers. Caterpillars, an important food (Chapter 39), were rare with the exception of newly hatched tent caterpillars, which Prairie Warblers were seldom seen to eat.

Sweep-netting of the shrub layer often collected no arthropods, but sweeps of White and Jersey Pines sometimes produced many small adult jumping plant lice (Psyllidae: *Trioza tripunctata* [Fitch]). Prairie Warblers newly arrived on territories with pines spent much time feeding in these, apparently eating nothing but psyllids. They also ate many tiny nymphs of the psyllid *Calophya nigripennis* Riley (both psyllids kindly determined by Louise M. Russell). Such small items probably yielded a low energy intake relative to foraging effort; similarly, the small spiders, flies, and Hymenoptera often eaten in this period (see Chapter 39) must have been less productive of energy than the larger items such as caterpillars that were available later. Between arrival day and the time when leafy vegetation became luxuriant there were substantial changes in foraging behavior (see Chapter

TABLE 3
TIMING OF REPOPULATION OF TERRITORIES¹ BY MALES² IN 8 YEARS

Date of earliest arrival	Number of males arriving on territory per day, ³ beginning with day of earliest arrival																
	day 1	day 2	day 3	day 4	day 5	day 6	day 7	day 8	day 9	day 10	day 11	day 12	day 13	day 14	day 15	day 16	day 17
20 Apr 58	1	4	3	0	2	3	0	1	2	0	0	4	2				
18 Apr 59	2	3	0	0	1	2	7	1	2	1	0	1	2	1			
16 Apr 60	4	1	0	1	1	2	4	0	1	0	2	1	1				
21 Apr 61	3	1	3	6	2	3	0	0	1								
22 Apr 62	2	0	0	4	4	1	0	3	0	1	0	1	1	0	0	1	
17 Apr 63	2	3	1	0	2	0	0	2	0	0	1	0	0	0	4		
16 Apr 64	4	1	2	3	2	3	0	1	0	0	0	0	0	0	1		
11 Apr 65	1	0	0	0	0	0	1	2	2	1	0	1	2	0	0	0	1
Totals	19	13	9	14	14	14	12	10	8	3	3	8	8	1	5	1	1

¹ See text, this page, for the standards determining the period of repopulation.

² Only males that acquired mates are considered.

³ Until the end of the period of repopulation (footnote 1), 0 indicates days on which no new male arrived on a territory. After repopulation was complete, daily spaces are left blank.

39), and it seems likely that the first Prairie Warblers returned about as early as the environment could provide food to sustain them.

TIME REQUIRED TO REPOPULATE STUDY AREA

Males: methods.—I have analyzed the time required each year for the study area to be reoccupied, using data from 1958 through 1965, when many arriving males wore bands put on in previous seasons. Unbanded males could usually be kept track of as individuals from day to day because of vocal and (sometimes) plumage differences and continuity in behavior. A bird is considered to have acquired his territory on the day he appeared on it, unless he soon moved away (see Chapter 5); an individual is counted once for each year he was present. The process of repopulation is treated as complete either (1) when all territories that were eventually to be occupied that year were taken by the males that first gained mates on them or (2) when 10 days passed without a new male's having taken up a territory, whichever was earlier.

Males: results.—Of the 143 cases of arrival shown in Table 3, 79% fell within 9 days of (and including) arrival day, despite considerable variability in the 8 years tabulated. In most years more than one male arrived simultaneously at the beginning of the season; 1965, when the earliest male was alone on the study area for 6 days, was unique. The irregular, wave-like progress of repopulation that is evident in Table 3 can be correlated to some degree with changes in weather. Weather doubtless largely accounts too for the differences in length of the period of repopulation, which varied from 9 to 17 days.

Years with late arrival days (e.g. 1961) may have tended to have short periods of repopulation and years with early arrival days (e.g. 1965) to have long periods; but exceptions (e.g. 1962) prevented a significant correlation in my small sample.

Females: methods.—Females sometimes moved around before pairing (p. 88); that and the fact that few banded females returned (Chapter 37) render data for females less precise than data for males. Table 4 shows only numbers of

TABLE 4
TIMING OF ARRIVAL OF FEMALES¹ ON STUDY AREA IN 7 YEARS

Date of earliest arrival	Number of females arriving per day, ² beginning with day of earliest arrival															
	day 1	day 2	day 3	day 4	day 5	day 6	day 7	day 8	day 9	day 10	day 11	day 12	day 13	day 14	day 15	day 16
24 Apr 58	1	1	0	1	1	1	0	5	5	0	2	1	0	1		
24 Apr 59	1	1	2	1	1	2	2	7	2	2	1					
22 Apr 60	1	0	1	2	3	1	3	0	0	1	1	0	0	1	2	
23 Apr 61	3	2	0	1	0	1	1	2	3	0	1	0	0	3	2	
28 Apr 62	6	2	0	3	1	0	3	1	1	1	0	1	0	1		
21 Apr 63	1	0	0	0	0	1	0	1	0	0	3	2	1	0	5	2
22 Apr 64	2	3	2	1	3	3	0	0	0	2	2	1	1			
Totals	15	9	5	9	9	9	9	16	11	6	10	5	2	6	9	2

¹ Females were counted even if they later left the area without pairing. See text.

² Days on which no female arrived are shown as 0 until all males with known pairing dates had acquired mates; subsequent days are left blank.

females arriving on the study area each day and doubtless includes some birds that did not remain and pair. A few unbanded individuals may have been tabulated twice. Defining the terminal date of the period of arrival of females created a problem, because females much more than males continued to appear and to pair throughout the season (Chapter 30). A few individuals that arrived in the last half of May and formed bonds with polygynists were arbitrarily omitted. In view of these several difficulties, Table 4 is only an approximate representation of the timing of returns of females from 1958 through 1964.

Females: results.—No striking difference in rate of return of males and females is apparent, but female arrival was a little more protracted and varied annually a little more. Only 70% of the 132 female arrivals fell in the first 9 days. While the largest influx in 1962 occurred on the first day a female was seen, in 1963 it occurred on the 15th day. The longest arrival period of females in any year was 16 days, the shortest 11 days.

INDIVIDUALITY OF RETURN SCHEDULES

Males: methods.—To learn whether individual males were consistently early or late arrivals (see Nice 1937: 51–53, Nero 1956: 6), I considered data from 19 males that returned in at least 2 years subsequent to the year of banding. All had been banded as adults.

Because of annual variation in date and pace of arrival, actual return dates were converted to relative figures. For this purpose, each annual period of repopulation was divided into three subperiods, and every return was assigned to a subperiod. Ideally about 33% of the arrivals would fall in each subperiod, but multiple returns on a single day (see Table 3) made it impossible simply to divide each year's cases into an early, a middle, and a late 33%. Instead, with the exception of 1962 and 1965, subperiod 1 in each year consisted of arrival day and the two following days; subperiod 2 consisted of the next three days; and subperiod 3 consisted of the remainder of the period of repopulation. Subperiod 3 is therefore longer than the others; but this tends to offset bias stemming from the fact that most males, and particularly old males, arrived in the first 9 days of the period of repopulation. In

1962 and 1965 the period of arrival was unusually prolonged, and no birds returned for a considerable time after the appearance of one male on arrival day. Therefore, I fixed three subperiods without regard to length but simply to include about 33% of the arrivals in each.

Two tests of the data were made: (1) Only the two initial returns of each male were considered, regardless of the number of years he was present. Under the hypothesis that the timing of the individual's returns would show no consistency from year to year, a male's two returns would have twice as great a chance of falling in different subperiods in successive years as of falling in the same subperiod. (2) All of each male's returns were considered, and each year in his series of returns was compared with the year preceding it. Thus, a male that arrived five times yielded four returns, to be classed as consistent or inconsistent with respect to the immediately preceding year.

Males: results and discussion.—In the first test, 13 of the 19 males (69%) were consistent. Applying the binomial test, $P \cong 0.002$. In the second test there were 42 cases, 26 of them (62%) consistent. With an expected consistency of only 33% under the null hypothesis, adj. Chi-square = 18.9; df = 1; $P < 0.001$.

Several individual histories corroborate these statistics. A male that arrived late in his first season, when perhaps he was a yearling, returned on arrival day in the next 5 years. Another male did the same thing in a later series of 5 years. These cases are especially impressive: weather or other chance factors might delay a bird's return in 1 or more years, but that such factors could cause early returns year after year seems out of the question. Consistent patterns of return were also shown by males that arrived later. For example, a male that returned twice did so on day 7 in both years. Another, which returned on days 9, 6, and 9, had to be classified under the system used as twice having been inconsistent, but his cases do not suggest random timing of arrival.

Among factors that might be conducive toward consistently early or late return are differences in threshold of response to the stimulus (stimuli) for migration, distance traveled, location of winter home range, flight speed, and time spent resting (possibly health). It is impressive that the mechanism timing arrival is sensitive enough to produce consistency even within the brief periods of repopulation found in this study.

Females.—Data for females cannot be tested statistically, because of the few returns of banded birds. Turning to individual histories, a female that came back four times was the first of her sex seen in each year she returned. Four other banded females also suggest the existence of individual differences: One returned on day 11 and day 9 of the female arrival period, another on day 8 and day 5. A third returned three times, on days 8, 7, and 1. The fourth was found on days 8 and 16.

HOURLY OF ARRIVAL

The time of day at which resident males probably arrived could be ascertained with considerable confidence for three reasons: (1) Males were immediately conspicuous because of their songs and the reactions they evoked in other males; (2) a high proportion of banded males returned, so that prompt identification of

individuals was possible; and (3) males evidently went directly to the territories of the previous year (see Chapter 5). None of these reasons is applicable to females, and this section deals only with males.

Indications are that some males arrived on their territories at night and that others did so between dawn and about 1030. There was little evidence that males arrived in the afternoon, but some were first found on their territories after an inspection by me in midmorning and before another in midafternoon.

The following cases involved banded birds; in all I had inspected the territories repeatedly on the day preceding arrival (as late as dusk in most instances) and had found them apparently unoccupied. (1) In three cases banded males began to sing as it grew light in the morning, and in 16 others they were singing when I arrived on their territories within 1–2 hours of daylight. (2) In 10 additional cases males began to sing (as late as 1030) when I had been on or near their territories for at least 1 hour after daylight and had detected no previous sign of their presence. This suggests that they had just arrived, a view strengthened in some cases by the fact that neighboring males appeared to react unusually aggressively to the singing, as though the singer were unfamiliar.

Instances in which unbanded males appeared to have come in during the night, or to have taken up territory within a few hours of daylight, were also numerous.

These observations lead one to speculate that some male Prairie Warblers reach their destinations in the night and that others land at night short distances from their goals. These latter evidently are able to and do continue oriented movement in the day and arrive at their destinations. Behavior sometimes observed in unbanded transient males may be examples of such postdawn movement toward a previous year's territory. A male that was the first Prairie Warbler seen in 1959 (therefore probably an old male) was foraging extremely rapidly near the ground at 0700. After 24 min of feeding with unusual speed, he flew to a perch at 8 m, headed southwest while continuing to climb, and flew straight away until he vanished at a considerable distance. There was no Prairie Warbler habitat within at least 3 km in the direction the bird took. In several other cases, these long, unswerving dawn flights from the study area were in southerly directions.

CHAPTER 5

SELECTION OF THE BREEDING SITE

MALES OLDER THAN ONE YEAR

Reoccupation and relocation of territory.—In 75 cases color-banded males came back to the study area after having bred there previously. Many males returned in more than 1 year and the 75 cases were produced by only 33 individuals. This section analyzes the frequency with which these birds settled on the territory of the preceding year and the circumstances in which the former territory was not selected. The section therefore deals with a facet of site fidelity, other aspects of which are dealt with in Chapters 30 and 37.

A male is said to have “reoccupied” a former site if his territory overlapped that of the preceding season. Otherwise he is said to have “relocated.” Relocation is a subject of unusual interest, because it is almost certainly one mechanism by which the species has dispersed into newly created habitats (see Chapter 1).

Of the 75 cases in which males returned, in 55 (73%) they reoccupied the former territory. In 51 of these 55, all observed territorial behavior was confined to that territory and to small areas adjoining it. The other four males were first seen on their former territories, then behaved territorially in other locations for 1–5 days but returned to occupy the former territories and breed. The distances separating the preliminary and the permanent sites of these four ranged between 200 and 500 m, and the mean was 350 m. On their preliminary territories the males advertised normally but did not acquire mates. As will be described, some banded males relocated permanently to new territories; the short-lived occupation of preliminary territories seemed intermediate between reoccupation and relocation. Occupation of temporary territories at the beginning of the breeding season was also seen in about 25 unbanded males that established themselves on the study area for 1–3 days in April but then disappeared. There was no observed fighting or other evidence of eviction.

In about 90% of the 55 reoccupations, the current territory overlapped the preceding territory by at least 80%, as would be expected from the fact that vegetation and shapes of fields considerably affected the general layout of territories (Chapter 29). However, some reoccupying males vacated large parts of former holdings and substantially shifted the center of their activities, in most cases with no evidence that pressure from neighbors caused the shifts.

Twenty males (27%) returned during the period of repopulation and relocated their territories. Six simply disappeared permanently after I had observed them for one or a few days, whereas I found the others on their new territories or saw them on the study area in later months or years. Although the six that disappeared may have died rather than relocated, this seems an unlikely explanation for any single case (see Chapter 38) and a highly improbable one for all six. I assume that these males went to new breeding sites beyond the study area.

In addition to the 20 instances of relocation from territories on the study area, a male that had left the area (i.e. presumably relocated to a territory outside its bounds) returned to it in a later year, taking up a site he had never held before. In the total of 21 cases of relocation, three individuals provided two cases apiece.

Circumstances attending relocation.—Thirteen birds returned to old territories and then within 2 days left them to relocate. Seven others stayed 3–8 days before leaving; the interval before one departure was unknown. All these males had advertised and otherwise behaved normally before moving.

All 21 relocations occurred either before females returned or at the very beginning of repopulation by females. Abandonment of the territory cannot, therefore, be attributed to inability to obtain a mate there. There was no apparent pressure from other males to relocate; indeed, many males that left last year's territories did so before any adjoining land had been occupied. Further indication that shifts were not forced is the fact that as old residents these males would have had little difficulty in holding, or retaking, former territories from usurpers (p. 40) and would have been subjected to fewer territorial challenges by males that had been their neighbors in the preceding years (p. 41).

The time between the departure from the former territory and occupation of the new was 24 hours or less in 13 cases, suggesting that leaving the former territory was not associated with any physiological inability to behave territorially. In the other two instances for which I have information, 5–6 days passed before the new territory was acquired. In both of these, a temporary territory was established for 1–2 days before the permanent site was taken; and other interim sites may have been occupied briefly.

In the 12 cases in which I found the new territory, the approximate distances between nearest boundaries of old and new were 10, 25, 50, 60, 200, 285, 300 (two cases), 800, 1500, 1600, and 3400 m (mean, 710 m). Some males whose new territories I found crossed barriers such as woods, cultivated fields, and suburbs. Only five selected the nearest Prairie Warbler habitat in the direction in which they shifted; the rest passed over suitable land and chose sites farther away.

I knew the ages of only two males that relocated. Both I had banded as nestlings, and they relocated to new sites on the study area near the beginning of the second breeding season.

The tendency to shift to a new territory seems to have been present throughout life. That relocation occurred at all ages is shown by data from 10 males I had banded at unknown ages. All were present at least three summers and their relocations took place at the following stages of my study of them: beginning of second year, four males; beginning of third year, one male; beginning of fourth year, three males; beginning of fifth year, one male; beginning of sixth year, one male. Of the three males that moved twice, one did so at the beginning of his second and fourth seasons under study, another at the beginning of his third and fourth seasons, the last at the beginning of his fourth and fifth seasons.

Related to the question of effect of age on relocating is the question whether the tendency to leave a territory varied with increase in the number of years a male had occupied it. Table 5 presents the data. There is no clear tendency toward change with the passage of time and certainly no indication that fidelity to a territory strengthened with the number of years of occupancy.

TABLE 5
NUMBER OF YEARS OF CONSECUTIVE OCCUPANCY OF TERRITORIES BY MALES¹

	Consecutive occupancy				
	2 years	3 years	4 years	5 years	6 years
Males with opportunity to occupy same territory, ² N	33	16	8	4	2
Males that did occupy same territory, N	22	13	4	3	1
Percent	67	81	50	75	50

¹ A territory was occupied by the same male in consecutive years if the boundaries overlapped to any extent in the years in question and if each year the male had a mate that nested.

² A male had opportunity to occupy the same territory in consecutive years if he remained on his territory for the rest of the breeding season in which he was first caught and survived and returned to the study area in one or more later years. The table does not show consecutive years of occupation of new territories to which males relocated; see text.

Reoccupation and relocation appeared independent of previous reproductive success or failure on a territory. Six males relocated from territories on which they had produced nest-leaving young in the preceding year, and six others relocated in a year following failure to bring off young. In the population as a whole, an estimated 41% of all males failed to produce nest-leaving young during a single season (see Chapters 32 and 33; see Table 133).

Only one of the 20 territories on the study area from which males shifted failed to be taken over by a new occupant within a few days, and this territory was occupied in later years. The more or less discrete patches of habitat that made up the study area differed from each other in size, age and composition of vegetation, degree of isolation, topography, and surroundings; but all but one patch were abandoned at least once. Further, the number of territories abandoned per field was roughly correlated with field size and number of territories present. Therefore, relocation was not necessarily associated with suitability of the habitat or with peculiarities of abandoned sites. Nor, in the cases of the 12 males whose new territories I discovered, could I see any pattern of differences between the abandoned territory and the new one selected.

Discussion.—Male Prairie Warblers appear to have the advantages conferred by fidelity to the breeding site (see Howard 1960) while also possessing the capacity to seek new, more suitable, territories. Inflexible site fidelity would clearly be disadvantageous to a bird that inhabits seral stages potentially of shorter duration than the life of an individual. Mayfield (1960: 53) has described in the case of the very rare Kirtland's Warbler how "[i]solated males sometimes have been found to be survivors of former colonies, clinging to their territories although the habitat is no longer suitable In two colonies followed to the end, the next-to-last year brought several males but few females, and the last year in each brought a lone, unmated male." I believe that such behavior would not occur in the Prairie Warbler.

Viewed as one mechanism by which Prairie Warbler populations disperse, relocation is of special interest because the actors are adults. Dispersal by adults is regarded as rare among passerines (see von Haartman 1949: 57–58), as it appears to be among vertebrates in general (see Gerking 1953, 1959, and Gunning and Shoop 1963, for fish; Twitty 1959, for newts; Howard 1960, for all vertebrates,

particularly mammals; see also Myers and Krebs 1971, for *Microtus* spp.). Indeed, in a review of dispersal of individual vertebrates Howard (1960) defines the subject in terms of movement from the "point of origin" of the animal to the site at which it settles to reproduce.

Howard (1960) has proposed that dispersal of vertebrates is innate in some individuals and/or species and "environmental" in others. Environmental dispersal is marked by only minor shifts in location, is density-dependent, causes relocation no farther than the nearest suitable available location, involves animals having a strong homing tendency, and may take place more than once in the individual's life in response to its need for space, a mate, food, etc. Innate dispersers make a single, quick, sometimes long move as the result of a short-lived, density-independent impulse "associated with the maturing of the sex organs" (Howard 1960).

Relocations of male Prairie Warblers do not fall easily within either of Howard's categories, but they more closely resemble his innate dispersal. Suitable sites are abandoned by the very males most able to retain them in the event of crowding; relocation is not associated with inability to attract a mate or with unsuitability of the site; males do not move simply to the nearest unoccupied habitat. And although Howard associates his hereditary dispersal with arrival at sexual maturity, the annual regression and development of the gonads of birds is not unlike the repeated attainment of sexual maturity by the same individual.

Among the selective advantages Howard attributes to the possession of the proposed innate dispersal mechanism are the ability to move rapidly into newly available habitat; this tends to result in discontinuous distribution of the species. The Prairie Warbler has demonstrated in recent decades that it has this kind of colonizing ability to a remarkable degree (Chapter 1).

Stability of male populations.—In combination, relocation of territories and annual mortality caused a 53% mean annual turnover in the identity of males on the various territories. Reoccupation of a territory by its tenant of the preceding year took place in 55 of 117 cases (47%) in which I had information.

Examples of stability and turnover are taken from 1964 and 1965: In the former year a tract was occupied by six males; three were in their fifth year as neighbors along common boundary lines; one was present for the fourth year, another for the third, and only one for the first time. In 1965, four of the males returned, but one relocated within the field and two relocated to different fields.

MALES IN THEIR FIRST SPRING

This section refers to movements of yearling males preliminary to occupying a breeding territory. Data on attachment to the hatching site are considered in Chapter 37.

Only one banded yearling was found at the very beginning of the breeding season. He advertised on two preliminary territories, spending 2 days on each; they were 1500 m apart. He then took over a territory 750 m from the second of the two preliminary sites. Such tentative initial occupancy was probably typical of young males, judging from a number of occasions on which males with traces of yearling plumage held early territories briefly. Vulnerability to eviction by returning former occupants probably added to this moving about.

However, as already noted, old birds sometimes moved in the same way. The yearling referred to in the preceding paragraph also moved twice when he was 2 years old. After returning, he left his former breeding territory and went to his first temporary territory of the year before; 4 or 5 days later he traveled 1800 m and relocated on a new territory. There were similar cases.

FEMALES OLDER THAN ONE YEAR

Factors affecting the breeding sites chosen by females differed from those influencing males in at least two ways: (1) Whereas probably all surviving males homed to the territory of the preceding year, a large number of females did not (Chapter 37). Analysis of sites selected by the limited number of females that returned to the study area necessarily leaves out of account females that did not exhibit this site fidelity and ignores what may be the most interesting aspect of female selection of breeding locations. (2) For a female, selection of a breeding site also involved the critical matter of finding and selecting a mate (see Orians 1969). Therefore factors controlling the female's choice of location were probably more complex than those governing the male's (see also Chapter 11, dealing with pair formation).

Reoccupation of site of preceding year.—In only 14 of 137 cases (10%) for which I had the necessary information did a female reoccupy and nest on her breeding home range of the preceding year; that is, the territories of her mate(s) in successive years overlapped. Three individuals occupied sites for 3 consecutive years and thus supplied two cases each. In all but one of the 14 cases reoccupation was at the beginning of the season, as defined on page 89; the exceptional female moved to her old site and her former mate in July and raised a second brood. The 10% reoccupancy rate for females is to be compared with 47% for males. It should also be noted that 65% of all breeding females were at least 2 years old (see Chapter 38).

In the remainder of the 137 cases, the female nesting on a territory was either unbanded and therefore known to be new to the study area (100 cases) or banded but at a different location than the one occupied previously (23 cases). Thus of 37 cases in which banded females returned to the study area and nested, 14 (38%) occupied the former home range. As noted above, the comparable figure for males is 73%. Some first nests of the current year were strikingly close to the builder's last nest of the year before; e.g. one was 12 m distant, and six were within 37 m.

Two of the reoccupying females did not pair with mates of the preceding year, although they were present; these females joined males holding territories that overlapped those of the former mates. One former mate had already acquired a female and was courting her, so that remating would not have been expected. But the other returning female was courted by her former mate and rejected him in favor of a neighboring male (see also pp. 98–99).

Reoccupation of site of a remote year.—One female nested in 1962 on her home range of 1959, 80 m from her nest of 1959. In 1960 and 1961, she had spent 4 and 5 days, respectively, in early spring on this same site without nesting and had then deserted the male there and left the study area.

Selection of a new site.—As noted, in 23 of 37 recorded cases (62%) a banded

female returned and failed to reoccupy her last year's breeding site. If the case in which reoccupancy was delayed until July is subtracted, the rate is 59%. Only 9 of the 23 females remained on the study area; these nested 260–2350 m from their last nest of the preceding year. The others presumably bred elsewhere; 10 of them were seen later, thus establishing that their disappearance from the study area was not the result of death.

Three females nested on the study area in one year, reappeared briefly next season but left, then returned after a 1-year absence to nest at a new site (260–1550 m from ones occupied previously).

One female bred on the study area in 1957 and 1961, in nests about 500 m apart.

Factors possibly associated with selection of new site.—In 14 cases in which banded females returned but then moved, I knew whether a male was available on the former breeding home range at the time the female arrived. In eight of these a male was present but had already acquired a mate; on three home ranges no male had established a territory; on the remaining three an unmated male was present and advertising. Thus in 11 of the 14 cases, there were reasons for the females not to stay. By comparison, in all 13 instances of female re-occupation of former locations, an unmated male was present when the female arrived. It thus appears clear that females have less opportunity than males to express attachment to former breeding sites. Although polygyny might have been an available alternative to individuals with a strong attachment to the former site, until the completion of nest building most males were too preoccupied with one mate to be able (or to choose) to court a second female effectively (see Chapter 31).

In at least two instances females may not have been in physiological condition to pair for some time after arrival. In successive years the same bird, always the earliest arrival of her sex (p. 29), spent 4 and 5 days on a former site while the males there courted her diligently. Each time she then disappeared for the remainder of the year. Her preference for the place was demonstrated once again when she returned to it in spring for the fourth successive year and nested there.

Age did not appear to be associated with female changes of location. Two returning 2-year-old females did not change breeding sites, whereas three females of that age did so. One female at least 5 years old did not change, but three females at least the same age did.

FEMALES IN THEIR FIRST SPRING

The behavior of yearling females in selecting a site was not different from that of older birds. Four birds that had been banded in the nest returned in their first spring. All were first seen with the males whose mates they became. However, like some older birds, certain unbanded yearlings associated with males in spring and then disappeared within 1–2 days. This question is discussed further in connection with pair formation (Chapter 10).

CHAPTER 6

BEHAVIOR OF NEWLY ARRIVED MALES IN SPRING

MALES ARRIVING ON UNOCCUPIED LAND

Introduction.—The evidence is strong that males more than one year old upon arriving from migration went immediately to the territory of the preceding year (Chapter 37), and this chapter describes the behavior of banded birds in what were probably the few hours immediately following the end of migration. That behavior varied considerably, largely according to whether territories were already occupied by Prairie Warblers and whether the newly returned bird and any neighbors present had held adjoining territories in the preceding year. Yearling males were also observed probably just after they stopped migrating. Arriving somewhat later (Chapter 3), they tended to confront more entrenched, aggressive neighbors.

Three banded males arrived before they seemed prepared to behave territorially and for one or more days foraged quietly on or near the territory of the preceding year. They watched their neighbors silently and behaved much like migrants.

Cold or rainy weather reduced singing and fighting.

Earliest arrivals.—I observed eight early-arrival males that had no neighbors within earshot. All had held their territories the previous year. Two were found when they began to sing about 45 min after civil twilight, and the others were found at about 0700. All behaved similarly, moving steadily and sometimes very rapidly and low (never above 2 m) through the fields; most flights were quite short, covering 1–15 m. All but one male foraged and ate constantly; the eighth did so very little. Occasionally a male showed aggressiveness, e.g. by darting at a nearby Dark-eyed Junco. All sang irregularly and rather infrequently. Intervals of silence lasted 10–20 min, and even during bursts of song the frequency per minute was low (e.g. 23 songs in 17 min, 43 in 24 min). Some called Chek a few times. All but one disregarded former territorial boundaries, ranging over surrounding land and even crossing ravines or woods into other fields. For example, in 24 min a male covered 4 ha which had been part of 6 territories including his own in the preceding year. When other males returned in the days that followed, early arrivals confined themselves to progressively smaller areas until the arrangement of territories of the new season had taken shape.

The early-morning behavior described above changed little as the hour of day advanced, except that the tempo of moving and foraging slowed somewhat and song became less frequent.

Later arrivals.—Males that arrived in fields already partly occupied usually passed more quickly than isolated birds (e.g. within 15 min) into full advertising and sometimes engaged in vigorous fights with neighbors (see Chapter 7). They also sought higher perches (up to 14 m) both to sing and forage and spent less time feeding, resting, and reconnoitering outside former territories.

MALES ARRIVING ON OCCUPIED TERRITORIES

Circular pursuits—description: The behavior of a male that sought to evict a territory holder from all or part of the latter's territory, and the territory holder's reaction to this challenge, seemed considerably ritualized, resulting in a circular pursuit. The term also applies to the behavior of any two males that arrived apparently simultaneously on a site and sought to claim it. Of 29 observed circular pursuits, 19 were at the beginning of the breeding season, presumably immediately after the challenging male arrived. The others occurred later in the season, were of brief duration, and were less stereotyped; therefore they were intermediate between the circular pursuits of early season and persistent trespasses (see Chapter 7). In 22 instances at least one of the two males was color banded.

Fully developed circular pursuit consisted of more or less circular or weaving flight in which the early-arrival territory holder chased the challenger that was seeking to take over the territory. Usually the roles of pursuer and pursued never changed. In three of four circular pursuits observed between simultaneous arrivals, the role of the pursued was taken by the male that had held the territory in the preceding year.

Most pursuits began with few preliminaries and ended equally abruptly, but some developed late in a long fight (defined as in Hinde 1952: 21); twice what appeared to start as adjustment or defense of a boundary appeared to turn into an effort by each combatant to drive the other entirely away. Of the 19 pursuits during the period of resettlement, 18 were between males that had never been neighbors on the study area; in the 19th case both males were unbanded. Circular pursuit always ended with the disappearance of the defeated bird or his withdrawal to nearby ground. If the latter occurred, he usually returned intermittently for a few hours to challenge the victor.

All but two pursuits were in the morning. Encounters lasted from 2–3 min to 2 hours, sometimes with interruptions. Heights of flight ranged between 1 and 10 m and usually were under 5 m. Distances separating opponents were rather consistently 2–3 m; sometimes males flew almost side by side, in which case the pursuer was usually on the inside track. The area covered varied with vegetation and locations of territory lines of other males, which drove out both pursuer and pursued when they encroached; typical areas were 35 × 40 m. Often part of the ground covered was not claimed by the pursuer; the pursued made sallies from this ground and, if he began to prevail, shifted the path of flight farther and farther into the tract he sought.

Paths of flight were circular, elliptical, figure-8, or erratic. Undulating flight, butterfly flight, moth flight, gliding (see Chapter 7), and nondisplay flight at ordinary speeds were used; undulating flight and nondisplay flight were most frequent. Both birds usually flew in the same way; when one changed his mode of flight the other quickly conformed. At times the pursuer apparently tried to catch up with the pursued; this caused the pursued to quit displaying and to fly fast.

The frequency of perching varied and depended largely on the pursuer, which usually was the first to stop and perch. Flight was seldom interrupted as long as 30 sec; even in some pursuits lasting 1 hour the birds perched only about 5% of the time. In contrast, some flights covered only 20 m at a time, and the pursuit

was a series of short moves interrupted by longer intervals of perching. Perched males, usually some 10 m apart, often crouched tensely, wings out (Chapter 7). Sometimes both, and usually the pursuer, gaped slightly while perching; both at times flicked the wings. Most sustained pursuits were silent. Singing (both faintly and at full volume) was confined to periods of perching; group-B songs (Chapter 8) were commonest, and the pursued usually sang more than the pursuer. Chek and Seep calls were rare.

The pursued did not permit the encounter to lapse; when the pursuer landed (often by gliding to a perch), the pursued either also landed or turned and flew very near his rival, provoking a new chase. When both birds were perching, the pursued almost always resumed flight first; this generally stimulated renewed pursuit, but if it did not the pursued turned back and again flew very near the pursuer. This constant renewal of the encounter after the pursuer had begun to weary of it was a certain sign that the pursued would prevail.

Even when the defeated pursuer had withdrawn from the territory, if he returned for a final challenge he still acted as pursuer. In a few cases in which roles of pursuer and pursued alternated, the area in dispute was finally divided approximately along the zone in which the reversal of roles took place. Thus this alternating-role type of circular pursuit resembled the common fights in which males chased each other back and forth across a territory line; it was particularly like deep penetration back-and-forth flight (Chapter 7).

The similarity between the few circular pursuits in which roles alternated and several common boundary displays, e.g. back-and-forth skirmishes (Chapter 7), suggests the origin of the more ritualized pursuits in which roles did not change. In the various encounters in which males switch from attacker to attacked, alternation of roles is assumed to reflect alternation in strengths of attack and escape tendencies both within each participant and also relative to the other participant; retreat normally signifies predominance of the motivation to escape. The apparent incongruity in the circular pursuit, in which constant retreat evidently was associated with determined aggressiveness and usually ultimately led to victory, may be explained by the widely held view that many displays consist of behavior (here retreat) emancipated from the motivation (here escape) with which it was originally associated. Perhaps the pursued bird did experience a strong tendency to escape but did not withdraw because of the force of his site fidelity. His persistence must have had a strongly threatening effect on the challenged pursuer, as indicated by the latter's failure to fly rapidly, his stopping the pursuit, and his failure to use the more aggressive vocalizations of fighting males. Presumably the difference between the situation of the two males in a circular pursuit and the situation of males displaying at a boundary is that in the pursuit both fighters usually have well-founded territorial expectations (based on occupancy in the previous year and earlier occupancy in the current year) with respect to the entire site.

Circular pursuit appears not to have been noted in other parulids, although a few episodes rather similar to it are reported (Eaton 1958: 216; Stewart 1953) and several wood warblers engage in "circling" at boundaries (Ficken 1962a: 608-610; Ficken and Ficken 1965). But prolonged pursuit occurs in other passerines, and in the House Wren the pursued rather than the pursuer at times ultimately wins

(Kendeigh 1941: 26). Especially interestingly, Sedge Warblers in England return to the marsh before Reed Warblers do, and males of the two species fight for the same space when the Reed Warbler arrives. Brown and Davis' (1949: 78-79) description of this interspecific fighting, which the late-arriving, always-retreating Reed Warbler regularly wins, very closely resembles the circular pursuits of the Prairie Warbler. They attribute the fact that the chased bird wins to "the triumph of persistent wearing-down tactics" (see also Murray 1971).

Priority of possession: Outcomes of circular pursuits are here classified according to whether a participant had held the disputed territory in an earlier year and also according to sequence of arrival of the fighters. (1) *Former owner arrived first*: In all four cases in which males attempted to acquire territories from defenders that had held them in preceding years, the defender won. Fights were short; only one continued more than 2-3 min, and it lasted about 20 min. (2) *Former owner arrived second*: Of nine cases in which the owner the preceding year returned and found a male already on his land, the owner regained his territory quickly in 7 and did so after some delay in the other 2 (see below). Among the 7 cases of quick victory, the same individual was the loser in 3, being ousted from 3 territories in 5 days as old residents returned. Finally this male was left on the only territory whose former holder did not return. The case is of interest because the much-evicted male was old and was seeking to relocate from his former territory in a distant field. When he finally succeeded in finding a site that he could keep, he reoccupied it during the next 2 years. (3) *Former owner and other male arrived simultaneously*: In four cases a former tenant and another male apparently arrived during the same night or the same dawn. Three former tenants played the role of the pursued in circular pursuits; and all regained their land. One was the pursuer, and he lost and disappeared (except for a brief return 21 days later, when he fought for 7-8 min and then departed again). (4) *Former owner not involved*: Of two cases in which neither male had held the ground previously, the early-arriving defender (pursuer) won once and yielded part of the territory once. (5) *Former ownership unknown*: In one case in which the situation of the males in earlier years was unknown, the defender-pursuer was forced to share his territory.

Presence of a mate and nest: The two cases mentioned in the preceding paragraph under 2, in which former owners regained their old territories only after delay, are instructive. Both males that succeeded temporarily in resisting the returning former owners had females and nests on the land being fought for. In one, the early arrival had extended his territory 25 m onto the territory of his neighbor of the 4 preceding years in order to include the nest site of the early arrival's mate. The neighbor then returned, fought for the land on which the nest was located, and lost; but the nest failed 11 days later, and the males resumed their territory boundary of the preceding years. In the second, a male returned to a large field he had held the 3 preceding years. A male with no previous experience there had arrived 13 days earlier and already had a mate, which had just completed a nest. The former owner first crowded the early arrival into a small area around the nest; a week later the early arrival disappeared, leaving his incubating mate and the entire field to the former owner.

PHYSICAL CONDITION AND TERRITORY-HOLDING

Obviously a male's physical state affected his capacity to acquire and defend territory. Mentioned above (p. 37) are three individuals that for several days after arriving did not behave territorially. Somewhat similarly, late in the breeding season when some males had lost their aggressiveness, I saw males attacked well within their territories and dominated and chased by neighbors. For example, a male carrying food to his nest was driven and harassed by a trespassing neighbor, although males carrying food usually drove away trespassers immediately.

Seriously injured birds were almost never seen, but in early May a male that had been on territory for over a week became unable to fly more than very short distances. He could not obtain a mate (see p. 83). By mid-May a neighbor trespassed without resistance, and on 18 May the injured bird disappeared. He returned to his territory on 26 June, his injury apparently healed.

RELATIONSHIP BETWEEN PRIOR ASSOCIATION OF MALES AND FREQUENCY OF FIGHTING

On several mornings I was on a territory when a former owner began to sing for the first time and was unchallenged by early-arrival adjoining males that had been his neighbors in the preceding year. These episodes suggested that prior association between males might affect their behavior toward each other at the time of settlement.

To investigate this I formed 106 pairs or sets, each consisting of two males on adjacent territories. Some of the pairs had had a common boundary in the preceding year; in others, one or both males were newcomers and the pair had had no known previous association. In all cases I was on the territories of the two males during some part of the day on which the later arrival of the two appeared, i.e. the day on which presumably the males were least familiar with each other and with each other's territorial claims. I recorded all fights that I saw on that day. When the 21 observed fights are distributed according to whether the males had had a known prior association, there were 2 fights between 33 pairs of former neighbors and 19 fights between 73 pairs of males not previously associated. In a test of independence, adj. Chi-square = 4.5; $df = 1$; $P < 0.05$ (compare Tompa 1964: 26, Marler 1956: 75). The most likely basis of the individual recognition implied by this result, and the basis most consistent with my observations, is individual differences in song (see p. 68; compare Weeden and Falls 1959; see Marler 1960).

The two instances of fighting by former neighbors involved unusual circumstances, a fact that emphasizes that such fighting was not common: (1) When an old male returned, his neighbor's mate had begun to build a nest that encroached on the returning male's former territory; the males fought because the encroaching neighbor would not relinquish the location of his nest. (2) Male A arrived a few days after Male B, which for several days had been feeding in a large flowering tree on Male A's former territory. When Male A returned Male B fought him in this tree for a few seconds and then quickly flew to his own territory; the two immediately resumed the boundary line of past years.

If the conclusion (Chapter 4) is correct that male Prairie Warblers arrived while food supplies were barely sufficient, mechanisms minimizing the energy required to gain a territory and settle its boundaries would be especially advantageous. One of the presumable selective values of the site fidelity displayed by old males (Chapter 37) may be the relative ease with which they are able to resume occupation of former territories.

CHAPTER 7

NONVOCAL TERRITORIAL BEHAVIOR OF THE MALE

TERMS

This section describes the agonistic behavior, other than vocal, by which male Prairie Warblers maintained their Type-A territories (Hinde 1956: 342) against conspecific males. Reference is also made to behavior between the sexes when that may contribute to an understanding of male-male fights. Fight is defined as in Hinde (1952: 21); probably all fights were sexual, "serv[ing] to secure objects or situations indispensable for reproduction" (Tinbergen 1936).

Stereotyped postures and movements are called "displays and acts." Sequences of mixed stereotyped and nonstereotyped behavior were common and are termed "encounters." Other students of parulids have developed a terminology for visible behavior, which I have employed when similarities seemed to warrant it. According to Ficken and Ficken (1966b) agonistic behavior patterns seem to be evolutionarily conservative in *Dendroica*.

NONAERIAL DISPLAYS AND ACTS

Tense crouching, sleeking.—Tensely crouching males flexed the legs and feet and perched stiffly, body parallel to the ground. In extreme cases the belly almost touched the perch, the line of the tail extending that of the body. Contour feathers were progressively sleeked as intensity increased. Other displays often accompanied the tense crouch; see below. Males watching other males, or sometimes watching females, crouched. Males crouched before, during, or after fights (and sexual chases; see Chapter 10); both winners and losers did so. Motivation was probably balanced between attack and escape. Effect of the crouch on the opponent evidently was slight; attacks sometimes ensued after both males had crouched. Similar crouching and sleeking in American Redstarts is considered derived from flight-intention movements (Ficken 1962a: 615; see also Ficken and Ficken 1965).

Retracting the neck.—Tensely crouched males often pulled the head back between the shoulders and assumed a hunched appearance. Males that puffed (see below) also retracted the neck and were evidently at a disadvantage relative to the opponent. Retracting the neck appeared to reflect an increased escape tendency; the behavior may be derived from a flight intention movement (see Ficken 1962a: 614).

Head forward.—Some males in the extreme tense crouch (at times with the wings out; see below) thrust the head forward. As in the American Redstart, this probably was "indicative of a strong attack tendency" (Ficken 1962a: 614; see also Ficken and Ficken 1965).

Wings out.—Crouching males when apparently quite tense often held the wings away from the sides, primaries pointing backward and at times drooping slightly. The wrists were sometimes separated only slightly from the body (2–3 mm), but

at other times the forearm seemed fully extended (compare the figure of a Chestnut-sided Warbler in Ficken and Ficken 1962). Wings out was never dissociated from the tense crouch and sleeking. Once an attacked bird shot its wings out full length, and the attacker immediately withdrew. The behavior evidently is a flight intention movement expressing a strong attack tendency and tending to cause the opponent to flee or to refrain from attack (compare Ficken 1962a: 615, Ficken and Ficken 1965).

Gaping.—The bill was opened 5–7 mm at the tip for several (sometimes 15) sec. Gaping occurred in males only in association with tense crouching following intense encounters such as flutter-ups, grappling, and melees (see below); thus it was nearly always given after flight away from an opponent that the displayer had attacked or resisted strongly; the displayer then gradually closed his bill and the opponent did not attack. Sometimes birds in which escape tendencies seemed to prevail gaped (e.g. puffing males—see below); but the commonness of gaping after strenuous attack (and sexual chases) suggests it was usually associated with attack motivation. Ficken (1962a: 614) calls the American Redstart's gaping probably a "ritualized biting movement" and "basically an attack intention movement" (see also Ficken and Ficken 1966b).

Tail spreading and bobbing.—Fanning of the tail occurred too rarely to interpret; the maximum spread was about 30 mm. The characteristic downward tail bobbing of the Prairie Warbler often became more frequent and more pronounced in males watching and drawing closer to each other at a boundary, both before fighting and when not followed by fighting. A flight-intention movement, bobbing probably reflected dominance of a weak attack tendency. See Chapter 40; see also Ficken (1962a: 615–617), Ficken and Ficken (1965), Stewart (1953).

Wing flicking.—Slight, rapid wing flicks were sometimes seen in males drawing near a boundary prior to a fight or perching during a pause in a circular pursuit (Chapter 6). Flicking, a flight-intention movement, occurred both with and in the absence of tail movements and seemed to express a weak attack tendency. The behavior may not be a display and may have no signaling function.

Puffing.—Rarely males erected the body feathers and assumed a rounded puffed appearance, always when other birds (including an American Goldfinch, a Field Sparrow, male Prairie Warblers) suddenly landed near them. Some, possibly all, puffing birds also retracted the neck; retraction was conspicuous when the opponent was on a higher perch than the displayer. At least some puffing males depressed the tail to horizontal; some gaped. A male visiting his former territory puffed when suddenly confronted by its owner; for 6 min the two moved silently through a large tree, 1–2 m apart; the visitor puffed most of the time. Feather erection in the Chaffinch is a resting intention movement; fluffed submissive posture is a reversal of certain aggressive movements. It may be associated with a mild escape tendency and "suggests a studied care to avoid provoking the other [dominant] bird" (Marler 1956: 43–47, esp. 46). A similar fluff display is a courtship posture in some parulids (Ficken and Ficken 1962: 116, figure at 110; Ficken 1963).

Solicitation.—Twice males squatted, drooped the wings, elevated the tail 45° above horizontal, and raised the head with the bill slightly opened. This strongly suggested the posture of a female soliciting copulation; see page 283 for possibly

related behavior between mates. Once the display occurred after the displayer flew in moth flight (see below) to his boundary, where a neighbor had been singing. The displayer called Chek, solicited for 3 sec, abandoned that position and walked (not hopped) down a blackberry stem; hopped about in a slightly squatting posture; then flew away but immediately returned and engaged in parallel movement (see below) with the neighbor. In the second case, an unmated male at least 4 years old suddenly assumed a soliciting position while on midterritory. Immediately a small bird I could not see well flew toward the displayer from behind as if to land on him, but the displayer quickly turned and chased the bird out of sight. Ficken and Ficken (1962: 110, figure at 110) report similar behavior in male Golden-winged Warblers after defeat in boundary conflicts; see also Mayfield (1960: 46), Marler (1956: 118–120), Andrew (1961: 322, 347–348).

Simulated sleep.—A male newly arrived from migration watched a neighbor for 2–3 min, then approached him to within 60 cm. Suddenly the neighbor stuck his bill into the feathers of his back as though sleeping; this lasted 30 sec, the displayer rocking slightly and once raising his head a little. The other male perched motionlessly, back to displayer, and after 30 sec moved away. Concealment of head markings and adoption of a position the reverse of head forward suggest an appeasement display (compare Tinbergen and Moynihan 1952, Marler 1956: 45–46, Baeumer 1959, Höhn 1967: 226); but if this was such a display, its rarity is hard to explain.

Turning the back.—Males in boundary encounters several times perched normally but with back turned toward the opponent (see preceding paragraph). The next move of both birds was to leave the scene, usually later to resume the encounter. The behavior was brief, and its otherwise normal appearance raises the question whether it was display; but turning the back during or after a fight is unexpected, suggesting appeasement.

Crown raising.—Rapid raising of the crown feathers, followed by their slow restoration to a normal position, occurred only once or twice after fights but often when Prairie Warblers watched predators (compare Ficken and Ficken 1962, 1966b). In the Chaffinch, crown raising is regarded as a resting intention movement “associated with a moderate escape tendency held in check by various tendencies other than aggression” (Marler 1956: 155).

Treading the feet.—Twice males watching other Prairie Warblers in evident excitement repeatedly raised the feet alternately from the perch. This presumably was an intention movement. Freeman (1950) reports that Ovenbirds alternately raise and lower the feet in threat display.

AERIAL DISPLAYS AND ACTS

Displays in mode of flying.—Various exaggerated flights with wings stiffened were common displays of agonistically (sometimes sexually) motivated males. Air speed was reduced and the displayer revealed to any Prairie Warbler behind him more of the dorsal surface of body, wings, and tail than is visible in ordinary flight. The chestnut back patch probably became more conspicuous. Orians and Christman's (1968: 75–76) proposed origin of blackbird flight displays appears applicable to the Prairie Warbler's flight displays; see also Crook (1964: 85).

In undulating flight, the line of flight viewed from the side formed a series of crests or peaks a few meters apart, with troughs between these peaks; the wings did not rise much above horizontal but beat in little bursts, producing bouncing flight. The angle of the tail was depressed about 20° below normal, causing speed to slacken. The axis of the body was 35° – 45° above horizontal, head and shoulders higher; at times the back was arched. The tail was spread to about 40 mm at its tip, making the white outer rectrices more noticeable. This was a common display in territorial boundary encounters (below) and circular pursuits (Chapter 6). It was also seen in males obviously experiencing conflicting tendencies to move toward and away from danger, e.g. an observer at the nest; the conflict often caused them to fly upward at an unusually sharp angle, sometimes nearly perpendicularly, and the result was not unlike hovering.

Butterfly flight was more exaggerated than undulating flight; the wings beat less often but in greater amplitude. Viewed from behind, the wings formed a 90° -angle V over the back and probably formed an inverted V at the end of the downbeat; they were little or not at all folded against the body on the upstroke. Flight speed was very slow, with stiff, butterfly-like wing beats somewhat resembling the stiff beats seen in the display flight of the Yellow-breasted Chat. Butterfly flight was used occasionally in circular pursuits, frequently in flights from opponents after physical contact that had apparently ended in victory for the displayer (also in flights after the sexual chase; see Chapter 10). Thus, this flight very often preceded tense crouching with the head forward and associated displays. A change from undulating flight to butterfly flight apparently reflected more intense attack tendency.

Moth flight appeared to be an extension of butterfly flight, and was seen in the same situations; often the two alternated. The wings were held out stiffly and fluttered in a shallow arc, probably rising and falling only slightly from the horizontal plane. Air speed was slow (Kendeigh 1945, Ficken 1962a: 609; compare Ficken and Ficken 1965).

Butterfly and moth flights, although most often oriented away from the opponent (or female), were frequently performed by a bird that had just dominated or was dominating another or that at least was at no disadvantage; they may have represented a state in which attack tendency predominated slightly. The bird to which the display was directed did not attack and often followed the displayer in its own butterfly or moth flight (females performed flight-to-male; p. 84). These modes of flight may have stimulated males to avoid contact with the displayer while having an attracting effect on females. Compare a similar American Redstart display flight toward rather than away from the opponent (Ficken 1962a: 610).

Gliding resulted from stopping the wing beats briefly; air speed slowed. Gliding was often used just before alighting, also in making tightly banked turns in flight. (Males descending on females before a sexual chase often glided.) In the American Redstart, gliding away from the other bird is frequent immediately following territorial encounters, is generally performed by the first male that leaves the conflict, and probably deters pursuit; a gliding bird is never chased, but a male flying from an opponent without giving this display is often pursued (Ficken 1962a: 610).

Bill snapping.—This audible display was usually given only in flight (compare Ficken 1962a: 614). Males closely chasing other males and also small birds of other species snapped the mandibles several times, producing clicking sounds; snaps were heard occasionally during flutter-ups (see below). Captured birds snapped the bill when handled, apparently in a genuine effort to bite. Bill snapping is evidently ritualized biting (Ficken 1962a: 618; see also Ficken and Ficken 1962, 1966b).

ENCOUNTERS

General.—The form of an encounter was almost always controlled by its location relative to territorial boundaries. Encounters on one male's territory were usually very short, ending in withdrawal of the trespasser. At a common territory line, each male's attack and escape tendencies presumably approached equilibrium, ordinarily resulting in equality between the two birds and more prolonged fighting. There was an observable graduation in intensities of encounters, permitting them to be classified roughly; as one fighter behaved more aggressively, the behavior of the other often kept pace. Fights sometimes started intensely, skipping low and intermediate levels; they also broke off without escalating to more aggressive levels. Ordinarily in boundary fights either there was no differentiation in roles of the participants, or the males alternated roles rapidly.

The following descriptions are divided according to whether or not the fighters met at a boundary. Within each sequence, the order progresses from encounters of low to those of high intensity.

Encounters within a territory.—(1) Approach: A male detecting a trespasser sometimes approached slowly (especially very early in the season) and by short flights, at other times in headlong fast attack. Faint Seep calls were occasionally uttered. The territory owner might perch 1 m from the trespasser and inspect him silently or while calling Chek. When the trespasser moved, usually away from the owner, the owner almost always followed in a weak chase. Twice intruders flew into tall trees while territorial males sang in the tops. The intruders moved upward slowly until only 2 m below the owners, which quit singing; the intruders gaped and crouched tensely, then flew up and perched at the height of the owners, which immediately mounted 2 m higher. The intruders again flew up to the owners' level, gaped and crouched tensely. The owners then flew straight at the intruders, which turned and fled and were chased. Superior height may give an advantage in most forms of encounter; it does so in flutter-ups and supplanting attacks (see below).

(2) Fast chase: Very aggressive males flew as fast as possible at interlopers, especially persistent trespassers, and pursued them from the territory. Once a pursuer struck a trespasser in flight, and another drove the trespasser to the ground and seemed to pull its tail with the bill (compare sexual chases, Chapter 10). Some chases were silent; in others there were Rattles, Sputters, and fragments of group-B songs. After fast chases the victorious male occasionally called Harsh Cheks. Sometimes probably both pursuer and pursued called Seep; rarely the attacked birds Squawked. Bill snappings were also heard, probably from both males (compare Stewart 1943, Ficken 1962a: 617).

(3) Undulating-flight chase: When a trespasser was quite aggressive and persistent, both the attacking male and trespasser flew in undulating flight. A retreating trespasser upon reaching the territory boundary sometimes glided to a perch. Such chases were silent.

(4) Circular pursuit: Occasional very persistent trespassers did not leave the territory immediately and a circular pursuit (Chapter 6) followed; the pursuer in these was the territory owner.

Encounters at a territory boundary.—(1) Approach: Males aware of each other across a common boundary sometimes approached slowly, especially shortly after arrival in spring; the encounter often terminated after mutual examination from 30 cm apart; one such examination lasted 6 min. Wing flicking, tail bobbing, and possibly slight tail spreading were seen at times. Posturing usually was confined to weak crouching with neck retracted. Songs if any were usually group-B, often at half volume; Seep and Chek were occasionally uttered. More aggressive males approached rapidly, the tense crouch became increasingly exaggerated, and the displays associated with the crouch were often given. Such males were silent or sang faintly.

(2) Parallel movement: Males at a boundary often moved along it parallel to each other in hops or short flights, each occasionally making a shallow penetration of his opponent's territory but avoiding flight directly at the opponent. Some encounters lasted up to 10 min with no apparent change in level of aggressiveness, but usually after about 1 min the birds either left the boundary or began to trespass alternately in back-and-forth skirmishes (see below). Parallel movement ranged in height from almost ground level to 9–10 m; males stayed 1–15 m apart, usually 5–10 m. Flights were short, often undulating. Tense crouching and associated displays were seen, also wing flicking, tail bobbing, and gaping. Some males wiped the bill without having eaten; some seized food; the circumstances suggest displacement or redirection (Moynihan 1955). Group-B songs were commoner than group-A, often muted; calls (Seeps, Cheks) were rare, and many birds were silent.

(3) Supplanting attack: A male often flew at a perched antagonist at their common boundary; if the attacked bird yielded (usually retreating 1–3 m), the attacker landed on or near the spot vacated. When the attacked bird failed to yield, the attacker either veered off, turned back at the last moment, or if attacking from above continued flying down and past the attacked bird. The attacked bird sometimes jumped as though to fly but landed on the same perch. If he resisted and himself flew at the assailant, a flutter-up usually followed (see below). Vocalizations were much as in back-and-forth skirmishes, described next. Both males sometimes called Squeaks and Rattles.

(4) Back-and-forth skirmishes: These are subdivided into four apparently related forms: (a) Darting frontal attacks were commonest, resulting from supplanting attacks in which the males alternated roles. Fighting fluctuated back and forth across the boundary, often for 30 min. Also characteristic were darting flights directly at the opponent; short, twisting evasive flights; tense crouching, gaping, and extending the wings while perching. Calls were Squeaks, Rattles, and Harsh Cheks. Wiping the bill and seizing food were occasional (see above). Songs were often muted; loud song was given in flight at times. Such skirmishes occurred 1–10 m above the ground, but most were below 5 m. The strip within which the

fighters moved was 1–20 m wide, usually about 10 m. These darting fights were highly variable, and the display component often appeared slight.

(b) Persistent indirect advances were a form of skirmish perhaps related to circular pursuit: there was no alternation of roles in crossing the boundary, and sometimes the skirmish resulted in a permanent change of boundary. A newly arrived male usually began the fight; from a perch on his own territory he flew 3–4 m onto that of his neighbor, moving not toward the neighbor but on a tangent from him. Alighting, he perched on his neighbor's territory until attacked, then retreated in undulating flight. This behavior was repeated for minutes or hours, and sometimes the encroached-upon male quit evicting and conceded. Tense crouching and associated postures were seen in both males; bill snapping was occasional. The advancing of the trespasser in these cases was only slightly stereotyped, whereas his retreats were display flights.

(c) Highly ritualized encounters: These were common; both males used some form of display flight, especially very exaggerated undulating flight. The order in which the fighters took flight differed from that in darting less ritualized skirmishes: The escape movement often began before the attacker started his approach flight, and escape seemed to evoke approach flight (compare circular pursuits, Chapter 6). Similarly, the retreating male sometimes landed while the other was still advancing, which caused the advancing male to land immediately. The behavior then resumed quickly, but with roles reversed. Distances and heights were the same as in less ritualized skirmishes, but the fighters appeared much less excited. Calls were rare and not loud; songs, if any, were faint. Ficken (1962a: 609–610) says of the American Redstart's circling: "This display may have originated from an attack flight toward the opponent, but as the bird approached the opponent his escape tendency increased and he turned and fled. However, during the process of ritualization the motivation may have shifted somewhat so that the display now reflects an attack-escape conflict with a somewhat stronger attack than escape tendency." This view seems based on the assumption that the redstart's display originated as a single circling flight from and back to a perch. The two-stage flight of the Prairie Warbler suggests a possible different derivation of circling.

(d) High penetrating flights: Infrequently a male that had perched high and watchfully near the boundary flew at a height of 10 m or more, slowly, sometimes slightly undulating, deep into his neighbor's territory. The neighbor then flew equally slowly toward the trespasser, which made a large, circling turn and retreated, followed by the owner. Some encounters ended when the two reached the territory line; others were repeated from that point. But in some, the original trespasser kept flying toward the center of his own territory, his neighbor pursuing and becoming the trespasser. Both birds then turned in flight and flew parallel to each other and to the territory line, then circled with the role of pursuer and pursued once more reversed. Usually the flight then ended at the territory line. Compare some circular pursuits (Chapter 6); see Ficken (1962a: 612).

(5) Flutter-up: When an attacked Prairie Warbler moved toward his attacker instead of retreating, the result was a sudden hovering stop by both to avoid colliding; this was usually followed by an approximately upward (5–7 m) and then downward slow fluttering flight. In these towering flights and descents, the long axis of the body was nearly vertical, as in many hovering species (e.g. hum-

mingbirds). The fighters kicked and at times pecked and often were in physical contact; rarely they fell to the ground and grappled (see below). In occasional flutter-ups the birds were nearly stationary in the air. Some flutter-ups were mere descents from fights begun high in the trees; some ascents were not followed by fluttering descents. When males terminated the encounter at the apex of the flight, each typically descended in bouncing flight with wings open and beating stiffly (compare the aerial display of the Yellow-breasted Chat). After landing, the fighters usually crouched tensely, wings out, head forward, and gaping. In some flutter-ups males rose and fell several times without a break in contact, continuing 5–8 sec. There was an apparent advantage in being higher than the opponent; the lower bird could not kick without leaning over backward and had to break off contact in order to avoid falling to the ground. Cheks, Harsh Cheks, Squeaks, and Rattles were usual, indicating great excitement; some flutter-ups were silent. Loud fragmentary songs were uttered at times. Bill snaps were occasional. Flutter-ups were especially common after very excited back-and-forth skirmishes and quite rare except at boundaries.

(6) Grappling: Struggling on the ground was a rare sequel to flutter-ups. The fighters, which usually were difficult to observe, thrashed slowly and silently about, locked together and nearly motionless most of the time, one male on top of the other. The feet seemed to hold the opponent. Probably only the upper male used his bill; one was seen to pull the crown feathers and the leg of his opponent. Pecking by the upper male was always deliberate, rather than fast or frenzied, at times appeared more like an unsuccessful effort to seize the opponent than an attempt to strike him. The lower male probably confined himself to trying to escape that position; some fighters reversed positions two or three times. Some grappling was only momentary; the longest episode lasted 70 sec. Absence of overt excitement, of rapid striking, and of vocalization was a conspicuous feature. One male that I netted soon after grappling was bleeding slightly from the leading edge of a wing. Mayfield (1960: 45) saw Kirtland's Warblers grapple. "Their mandibles were interlocked deeply, and they lay on the ground motionless, with wings outspread. One was on its back and the other pressed down on it, pinning it there." See also Eaton (1958: 216).

(7) Melee: Highly excited, very rapid encounters among three or four birds usually lasted about 20 sec. Sometimes the participants were two pairs, sometimes three males at a common corner, sometimes other combinations. The birds seemed to chase each other indiscriminately (e.g. a male chased his mate instead of a neighbor) and may have lost track of the identity of participants because of the milling and rapid movement. Rattle, Squeak, and Whine were common; loud and fragmentary songs were also uttered.

(8) Circular pursuit: These are described in Chapter 6.

FACTORS ASSOCIATED WITH FREQUENCY AND KINDS OF INTRASPECIFIC ENCOUNTERS

This section analyzes 517 encounters between male Prairie Warblers before 21 July (1952–1963), after which territorial behavior was very infrequent. An encounter is counted only once and is classified at the most intense level reached.

TABLE 6
FREQUENCY OF INTRASPECIFIC ENCOUNTERS,¹ ACCORDING TO DATE AND
NUMBER OF DAYS MALES WERE TERRITORIAL²

	Date					Totals
	11-30 April	1-20 May	21 May-10 June	11-30 June	1-20 July	
Number of encounters ¹	91	214	85	89	38	517
Mean number of days males were territorial ²	7.4	19.9	19.4	19.1	17.0	82.8
Index of frequency of encounters ³	12.3	10.8	4.4	4.7	2.2	—

¹ The encounters analyzed are described on pages 50-51.

² See text, this page.

³ See text, this page.

Approaches are not included. If either fighter left the scene for less than about 3 min and then returned and resumed the fight, this is treated as a continuation of a single episode.

Date.—The season is divided into five periods, each 20 or 21 days long. The first period began on 11 April, the earliest date of arrival; the last ended on 20 July. The number of males holding territories varied according to date (see Chapter 31), which affected the frequency of opportunities to fight. To obtain a standardized unit with which to measure frequency of fights per opportunity, I selected 88 territories visited daily in the 7 years in which most males present were banded. The timing of field work was roughly comparable in each period and year. The total number of days on which the 88 territories were occupied in each of the 5 periods was determined, and the mean number of such days per period was obtained. The appropriate mean was then divided into the absolute number of fights in each period, yielding an index of frequency of encounters per period.

Table 6 presents the results, which require no discussion here but will be referred to below.

Mating status and frequency of encounters.—Table 6 shows that there were fewer fights after 20 May than before that date. The fact that fighting was less frequent in the portion of the breeding season (21 May onward) in which most males were mated (Chapter 11) suggests a possible cause-effect relationship, which this section investigates. It deals only with the 40 days (11 April–20 May) when fights were most numerous; 305 encounters were observed during that period and are distributed according to whether the fighters were both unmated, both mated, or one mated.

To obtain expected frequencies under the null hypothesis it is necessary to know the number of days males spent in each of the three status categories prior to 21 May. I therefore selected all cases (54) involving any two males whose boundaries adjoined and whose mating status I knew between the dates of their arrival and 20 May. I then asked how many days both neighbors (and potential antagonists) were present and both unmated, how many days was one unmated and one mated, and how many days both were mated. The 54 sets of males provided 3 means: both males were unmated a mean of 3 days; one male was unmated a mean of 5 days; both males were mated a mean of 16 days. The 3 means total 24 rather

TABLE 7
OBSERVED AND EXPECTED FREQUENCIES OF INTRASPECIFIC ENCOUNTERS¹
BETWEEN 11 APRIL AND 20 MAY, ACCORDING TO MATING
STATUS OF PARTICIPANTS

Mating status	Mean days ² adjoining males were present, per mating status	Encounters	
		Observed	Expected ²
Both males unmated	3	62	38
One male mated	5	70	64
Both males mated	16	173	203
Totals	24	305	305

¹ See pages 51-52.

² Methods are described on pages 51-52.

than 40 (i.e. the length of the period 11 April-20 May) because not all males arrived as early as 11 April. For example, Table 6 has shown that the mean number of days a male was on his territory between 11 April and 30 April was only 7.4 days, and that number is further reduced here because the status of 2 males per set is involved. The expected distribution of fights per mating status, if fighting is independent of status, is obtained by dividing the total number of fights by 24 and multiplying the quotient (12.7 fights) by the 3 means, 3, 5, and 16.

Table 7 indicates that frequency of fighting was significantly related to mating status or to some associated factor; Chi-square = 20.2; df = 2; $P < 0.001$. Males fought more when both were unmated. However, that may have been because that status was commonest when territories were being established and boundaries settled, and courtship did not yet occupy the attention of either. This latter point is discussed below.

Mating status and kinds of encounters.—Relative frequencies of kinds of encounters also changed after females arrived. Circular pursuits and the more intense forms of boundary fighting were the commonest fights before females returned; they decreased thereafter. As an example, the observed frequency of flutter-ups according to mating status of participants between 11 April and 20 May will be compared with the expected frequency (obtained as described above); observed numbers are stated first, expected numbers in parentheses: both males unmated, 8 (6); 1 male mated, 19 (11); both males mated, 23 (33). Flutter-ups, then, were significantly less numerous ($P \approx 0.01$) after males acquired mates. Results are similar for back-and-forth skirmishes and supplanting attacks. Melees, perhaps because by definition they included more than two participants, almost all occurred shortly after females arrived and were usually touched off by the appearance of one or both females near two males engaged in a boundary fight.

Stage of reproduction.—This subsection deals with stages of reproduction beginning with pair formation.

During pair formation fighting was often caused when a female crossed a boundary; also, males frequently trespassed to court or watch another male's mate, and this caused an attack. Fights remained frequent during pre-nest-building, when exploration for nest sites resulted in much movement over the territory and the female's searching appeared to interest neighbors and attract them to watch. Nest building had a similar attraction, but it occurred at a fixed location, often

TABLE 8
FREQUENCIES OF SELECTED TYPES OF ENCOUNTERS BETWEEN MATED
MALES, ACCORDING TO DATE

Encounter	11 April-20 May ¹		21 May-20 July	
	Observed	Expected ²	Observed	Expected ²
Flutter-up	23	8	8	23
Other boundary encounters ³	100	41	55	114
Chase of trespasser	10	35	122	97
Totals	133		185	

¹ See text, this page.

² See text, this page.

³ This category includes back-and-forth skirmish, supplanting attack, and parallel movement.

away from a defended territory line (Chapter 15); the builder's male also usually stayed near the nest (Chapter 16), which reduced contacts with neighbors unless they trespassed. Fighting therefore declined. For example, I watched two adjacent males for 31 hours distributed over 3 days, during which each acquired a female and the females began to search for nest sites. The males had 28 fights. Two days later building began simultaneously on the two territories, and the males fought only once in 7.5 hours.

The onset of laying in first nests immediately triggered nest predation and cow-bird parasitism; most nests that failed were replaced (Chapter 33), and soon the stages of reproduction of pairs were out of phase. Consequently it is impracticable to relate the incidence of fighting to the stages of reproduction from egg laying onward, but it is clear that fighting declined at this time (after 20 May; see Table 6). Further, accompanying this reduction, relative frequency of boundary fights dwindled greatly and evictions of trespassers became more common, as will be shown below.

Analysis is of 318 encounters between mated males and is restricted to three categories: flutter-ups, all other boundary encounters, and chases of trespassers. Fights of these three kinds are distributed according to the calendar intervals 11 April-20 May and 21 May-20 July, and changes in frequency of each kind over time are investigated. The differences in duration of these intervals must be taken into account: 16 days is considered the period during which two neighbors were both mated prior to 20 May (see above) and 44 days as the corresponding period after 20 May. Forty-four rather than 61 days, the length of time between 21 May and 20 July, is used because (1) some males lost females after 20 May and were unmated for various intervals and (2) many males ceased to be territorial before 20 July (see pp. 427-429).

Table 8 shows for each category of encounter a change in frequency. The results are consistent with the observation that boundaries had ceased to be the subject of intense fighting by the time eggs were laid in first nests.

The circumstances under which males trespassed and provoked encounters will be apparent from the following: Of 192 encounters between mated males, one of which was trespassing, about 80 started when a bird encroached to watch a neighbor's female as she built her nest. About 40 chases were caused by approaching the attacker's mate when she was foraging or searching for a nest site.

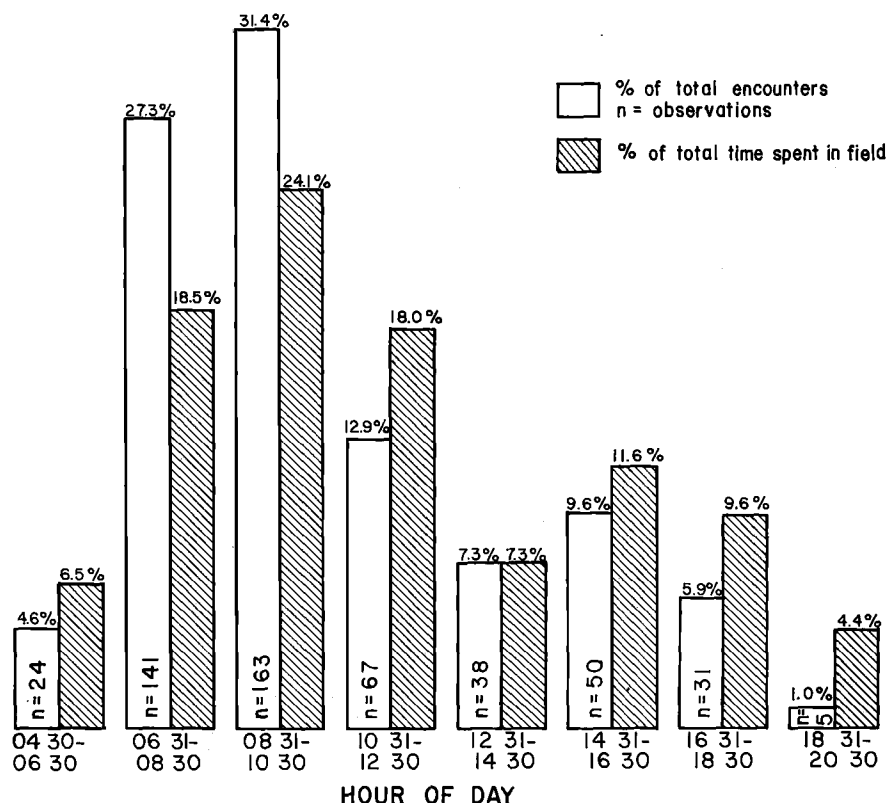


FIGURE 6. Distribution of 519 intraspecific encounters and of 5524 hours of field work, according to 2-hour intervals of the day. Encounters were nonrandomly distributed.

There were 72 encounters that resulted from trespasses in which attraction to a female seemed not involved: 19 trespassers ignored boundaries while tending their fledglings; 19 were exploring (see Chapter 30); 13 were relocating territories in midseason (see Chapter 30); 11 approached fledglings, evidently attracted by distraction displays of the parents; and 10 approached fledglings, evidently attracted by their calls.

Hour of day.—Fighting and time of day were significantly ($P < 0.001$) associated (Fig. 6). I assigned 5524 hours spent in the field between 15 April and 25 July (1952–1963) to eight 2-hour intervals beginning with 0430–0630 and ending with 1830–2030 and allocated the 519 encounters among these units. I was in the field at about the same times of day from April through July in the years involved and did not change methods of observation according to time of day. Fights before 0630 and after 1030 were fewer than expected if fighting had been randomly distributed; between 0630 and 1030 there were far more fights than expected. Trespasses were less frequent just following dawn than later in the day; among forms of boundary fighting there was no shift in relative frequencies as the day advanced. This subject is discussed further on page 59.

Weather.—Cool temperatures unaccompanied by rain did not inhibit fighting, nor did showers in warm weather. Rain and cold together, however, appeared to

reduce aggressiveness among males. These two conditions ordinarily concurred only in April and May. There were few fights in very windy weather; the decrease of song on windy days (Chapter 8) suggests that wind inhibited aggressiveness.

Previous encounters between fighters.—The facts that neighbors of previous years fought less than strangers when settling on territories (Chapter 6) and that boundary fighting became less frequent as the season advanced (above) suggest that familiarity with neighbors' boundary claims had the effect of reducing encounters (compare Hinde 1952: 83). However, over a short span, e.g. a few days, hostility generated by recent encounters often seemed to carry over, so that males resumed fighting more readily and fought more intensely because of recent experience. As an apparent example, two males fought 36 times at their boundary during 43 hours between 3 May and 9 May with no perceptible reduction in intensity and no change in boundary line.

Long-familiar neighbors seemed to trespass on each other as often as did strangers. Numbers of chases seen among 3 males whose territories adjoined for 3 years are evidence of this; numbers observed between each 2-bird combination are given in chronological order, beginning with the first year of their association. Males A–B: 1, 16, 2; males A–C: 2, 7, 4; males B–C: 1, 2, 4. All these chases were caused by trespasses to watch nest building; numbers of nests built per year were not correlated with these numbers of chases.

TREATMENT OF TRESPASSING FEMALES AND IMMATURE PRAIRIE WARBLERS

Females.—Except in melees, males were rarely hostile to females. Occasional aggressive reactions consisted of a close approach and tense crouch with head forward, wings out, and gaping; females reacted with these same behaviors. Causes of male aggressiveness at these times were not apparent.

Usually males courted and attempted to copulate with their neighbors' mates, including females tending fledglings. I caught several females and displaced them in cages to the territories of strange males; the females evoked no hostility. When I displaced broods of fledglings on to adjacent territories, the territory owners permitted their mothers to enter and feed them but repulsed their fathers.

Immature Prairie Warblers.—I frequently put fledglings newly out of the nest on territories of pairs that were not their parents; sometimes the young were fed by the territorial male, sometimes merely inspected or ignored, never treated hostilely. One male whose mate was incubating took over the care of a brood of 10-day-old young that I liberated on his territory.

The reception given to immature Prairie Warblers at or near the age of independence was observed only a few times because territorial behavior had waned by the date most young reached this age (see Chapter 34). Usually such young were tolerated. Independent immature birds occasionally attached themselves to broods that were in the last stage of dependence (38 days or older) and followed them about without being driven away by the adults (p. 437).

Three cases of aggression toward young birds consisted of repeatedly chasing a begging 35-day-old that entered from an adjacent territory, repelling a 57-day-old that persistently followed the attacker's mate as she explored for a nest site, and driving an independent fledgling of unknown age from the territory.

EXPERIMENTS WITH MOUNTED SPECIMENS

The skin of a brightly marked male Prairie Warbler, its position approximating the tense crouch, was sometimes used to test the reactions of other Prairie Warblers (or to lure them into a net). The experiments were crude but yielded some information.

The mount was never ignored, but reactions to it varied greatly. The mildest response (four cases) was to hover in front of and then over the mount and to fly around it silently in undulating flight. Two males lit on the mount and were so preoccupied that I was able almost to touch them. Just before flight to the mount these males crouched tensely with retracted neck and called Seep.

An unmated male advertising in May was presented with the mount at dawn. He ignored or failed to see it for 30 min, then suddenly dropped directly to its back and for 30 sec stood fluttering his wings in a large arc and pecking at the head. He then flew to a perch and sang. Next day he performed about the same acts, flying to the mount's back and remaining on it for 10 sec. This time, after having faced forward he turned and faced the tail, giving the impression of walking on the back. He then hopped off, perched with wings out, and flew in moth flight to the ground. This episode took place in silence. Gill and Lanyon (1964: 57-58) used a mounted Blue-winged Warbler in experiments on species discrimination. "The attacking male usually landed on the back of the mount and pecked at the crown. . . ." See also Hinde (1952: 71).

INTERSPECIFIC FIGHTING

Male Prairie Warblers made attacks on or were attacked by birds of 27 other species, all but two of them (Ruby-throated Hummingbird and Hairy Woodpecker) passerines. Among 157 observed encounters, 89 were with common resident species of the study area, 39 with residents of the margins of the study area, and 29 with nonresident migrant species. Details are presented in Table 9.

In 110 of the cases, a male Prairie Warbler appeared to be the aggressor and chased the other bird from his territory, or from a perch, or from the vicinity of the warbler's nest or female or fledglings.

Interspecific fighting was usually of low intensity and short duration compared to encounters between Prairie Warblers. Attacks on a bird of another species resulted in 70 chases, most of them short but some covering 40 m and accompanied by bill snapping. Once a Field Sparrow was struck 4-5 times on the back as it tried to escape. There was no territorial exclusiveness, hence no boundary fighting; but occasionally the kinds of fights that are usual at boundaries were seen, viz. 24 brief supplanting attacks and 11 flutter-ups or back-and-forth skirmishes.

In evaluating the high ratio of interspecific fights in which the Prairie Warbler was the aggressor, it should be noted that in most encounters with species dwelling on the margins of Prairie Warbler territories and in all encounters with migrant species the warbler was on the center of its territory and the other bird was off its territory or had none.

Size and color of birds fought.—There was a close negative correlation between the size of the other bird and the frequency with which the Prairie Warbler fought it. The most commonly fought species, arranged in a descending order that takes

TABLE 9
 INTERSPECIFIC ENCOUNTERS OF PRAIRIE WARBLERS, ACCORDING TO RESIDENCE
 OF SPECIES ENCOUNTERED

	Prairie Warbler aggressor	Other species aggressor	Totals
I. Common residents in shrub habitat ¹			
Blue-winged Warbler	14	7	21
Field Sparrow	17	11	28
American Goldfinch	24	3	27
Common Yellowthroat	4	1	5
Indigo Bunting	1	3	4
White-eyed Vireo	1	2	3
Yellow-breasted Chat	1	0	1
Cuckoo, 2 spp. ²	0	0	0
Cardinal ²	0	0	0
Rufous-sided Towhee ²	0	0	0
Brown-headed Cowbird ²	0	0	0
Subtotals	62	27	89
II. Rare residents in shrub habitat and common residents in woods margin ¹			
Blue-gray Gnatcatcher	12	2	14
Ruby-throated Hummingbird	0	5	5
Eastern Wood Pewee	1	2	3
Carolina Chickadee	3	0	3
Red-eyed Vireo	1	2	3
Kentucky Warbler	1	2	3
Summer Tanager	0	2	2
Hairy Woodpecker	1	0	1
Tufted Titmouse	1	0	1
Carolina Wren	1	0	1
Brown Thrasher	1	0	1
Bell's Vireo	0	1	1
Yellow-throated Vireo	1	0	1
Subtotals	23	16	39
III. Migrants and winter residents ¹			
Palm Warbler	11	2	13
Nashville Warbler	5	0	5
Yellow-rumped Warbler	4	1	5
Magnolia Warbler	3	0	3
Least Flycatcher	0	1	1
Black-poll Warbler	1	0	1
Dark-eyed Junco	1	0	1
Subtotals	25	4	29
TOTALS	110	47	157

¹ Species fought most often are placed first in each class, taking into consideration the number of opportunities Prairie Warblers had to fight them.

² For completeness, five common large species sharing the Prairie Warbler's habitat are included although no fights were seen.

into rough consideration their numbers and therefore the opportunities Prairie Warblers had to come into contact with them, were Palm Warbler (13 encounters), Blue-gray Gnatcatcher (14), Blue-winged Warbler (21), Field Sparrow (28), and American Goldfinch (27). The two cuckoo species, the very common Cardinal, Rufous-sided Towhee, Yellow-breasted Chat, and even the Brown-headed Cowbird were never attacked; and these larger species never attacked the warbler. There were, however, a few mismatches, e.g. a warbler attacked a Brown Thrasher.

Fights probably were more frequent with species marked somewhat like the Prairie Warbler. The numbers of attacks on the yellow American Goldfinch and Blue-winged Warbler are suggestive, as are attacks on species with white outer rectrices (Blue-gray Gnatcatchers, several migrant warblers).

Most attacked birds whose sexes I could determine were males, but that is probably attributable to the generally more conspicuous behavior of male passerines.

Fights with Blue-winged Warbler.—Fights with Blue-winged Warblers were more vigorous, prolonged, and suggestive of intraspecific encounters than were any other interspecific fights. Included were flutter-ups, back-and-forth skirmishes, supplanting attacks, and tense crouches with wings out and gaping; calls included Harsh Chek, Squeak, and Whine. A Blue-winged Warbler sang after a fight with a Prairie, and another joined in a melee with two Prairie Warblers.

Fights with Field Sparrow.—Field Sparrows appeared much attracted by Prairie Warbler nesting activities, and many encounters resulted from their habit of going to warbler nests and looking at the young in them. Still, the number of encounters seen usually was no more than 3 per year. The minimum distance between simultaneously active nests of the two species was 2.7 m. Some of the encounters may possibly have been caused by the great similarity between one song version of the Prairie Warbler and the song of the Field Sparrow (see pp. 60–61). A Field Sparrow once flew to within 1–2 m of a Prairie Warbler singing this version; judging from its behavior, the sparrow may have failed to recognize the song as a warbler's. Most encounters with Field Sparrows were brief chases or supplanting attacks; the chase in which a warbler struck a sparrow has been mentioned. Once a Field Sparrow landed beside a mounted warbler skin, opened its wings, and pecked the mount twice.

Fights with American Goldfinch.—All encounters with goldfinches were brief, all but 3 (of 27) were initiated by the warbler, and all but 4 led immediately to the rout of the goldfinch. Female goldfinches commonly removed material from nests of the Prairie Warbler. I saw this nine times, several of them in early May, long before goldfinches began to nest. Most nests that were dismantled were old, but a goldfinch once took material from a nest under construction, visiting it between the trips of the female warbler. No goldfinch was attacked while dismantling a warbler nest.

Fights with Ruby-throated Hummingbird.—The much smaller hummingbird chased or harassed a Prairie Warbler on five occasions. Twice a hummingbird approached to within 30 cm of a perching warbler and hovered before it, moving horizontally in a semicircle. Other hummingbirds approached flying warblers, which dropped instantly to low perches; the hummingbirds then hovered, and the warblers alertly and without posturing turned to face the moving hummingbirds. Once a warbler suddenly stopped watching and flew out of sight, the hummingbird in pursuit.

Timing of interspecific encounters in which Prairie Warblers were aggressors.—Total attacks by Prairie Warblers, according to month of the breeding season, were as follows, with the number of attacks on migrants in parentheses: April, 41 (14); May, 31 (11); June, 28 (0); July, 10 (0). Comparison of this distribution with that in Table 6 shows a good deal of similarity, even if the numbers of migrants

TABLE 10
NUMBERS OF INTERSPECIFIC AND INTRASPECIFIC ATTACKS BY MALE PRAIRIE
WARBLERS, ACCORDING TO TIME OF DAY

Object of attack	Time				Totals
	0430-0830	0831-1230	1231-1630	1631-2030	
Conspecific	165	230	88	36	519
Not conspecific	56	35	5	14	110
Totals	221	264	93	49	629 ¹

¹ Chi-square = 26.1; df = 3; $P < 0.001$.

are subtracted from the totals (because migrants were present only in April and May).

Numbers of interspecific attacks by Prairie Warblers, distributed according to 4-hour periods of the day beginning with 0430-0830, were as follows in chronological order: 56, 35, 5, 14 (see Table 10). The corresponding distribution of intraspecific encounters (Fig. 6) was 165, 230, 88, 36; in a test of independence, Chi-square = 26.1; df = 3; $P < 0.001$.

Two related explanations for this difference may be suggested: (1) The Prairie Warbler's aggressiveness was probably very high in the early part of the day, when agonistic behavior may have been more likely to be evoked by weak stimuli, i.e. birds that differed from Prairie Warblers. Correspondingly, aggressiveness evidently was low in the afternoon (note the very low frequency of interspecific fights at that time). (2) Prairie Warblers trespassed less in the early hours, when they were much occupied with singing on their territories and when nest building, a major attraction to trespassers, was often not yet in full swing for the day (Chapter 17). Because of the relative infrequency of intraspecific trespassers, territorial males may have been more prone to attack birds of other species.

CHAPTER 8

SONG

This chapter describes the general characteristics of Prairie Warbler songs and the circumstances under which some of them are uttered and provides background for other subjects treated in this work.

DESCRIPTIONS

General.—The individual male Prairie Warbler has a large repertoire. Like those of many other parulids, the songs of this species are of two basic types (compare Ficken and Ficken 1962: 112–114, 1965, 1967a; Gill and Lanyon 1964; Morse 1966, 1967); in the absence of any uniform terminology I call these “group A” and “group B.” Within each group are several considerably stereotyped variations, called “versions” (compare Armstrong 1963: 37–39, Gill and Lanyon 1964; Ficken and Ficken 1967a: 153–157). Duration of songs in the following description is approximate unless otherwise stated.

Group-A songs.—Group-A songs are the loudest uttered; under optimum conditions they became inaudible to me at about 185–200 m from the singer. The version usually described as “the” Prairie Warbler song is a series of short, equally spaced, rising, abrasive, jerky notes, typically about 15 in number, termed here the Chatter (see Fig. 7-A). Chatters were timed as lasting 1.0–2.5 sec.

When the notes are sung so close together that they virtually fuse, the result is a less harsh-sounding, high Trill (Fig. 7-B), lasting 1.2–2.2 sec. Intermediates between Chatter and Trill were heard occasionally. A final version, Sing-song, usually consists of three or four long, ringing, sometimes rasping notes rising to a crescendo in volume but uttered at about the same pitch, followed by a series of three to seven short notes ascending the scale but usually falling in volume (Fig. 7-C). The Sing-song thus is made up of two parts. Sing-songs are 1.6–2.3 sec long.

Group-B Versions.—Group-B songs are more numerous and less stereotyped than those of group A, fainter (inaudible to me beyond about 125 m), and less easily described (see Fig. 7-D, -E, and -F). I differentiate six versions; most, like Sing-songs, have two parts, a series of long notes and a series of short notes. The long notes are sung first most of the time; sometimes only half (the first or second) of the version is sung. Most versions when compared to group-A songs have longer, clearer, more whistled notes and/or slow, hoarse, rasping notes.

Many observers (e.g. Allen in Bent 1953: 434–435; compare Borror 1968) have remarked on the resemblance between a certain Prairie Warbler song (group-B version; see Fig. 7-D) and Field Sparrow songs.

Stein (1968) has analyzed modulation in Prairie Warbler songs.

DAILY PATTERN OF SONG

Dawn vocalizations.—Except when indicated, the following applies to mornings with clear skies and weather favorable for singing. I had no instrument sensitive

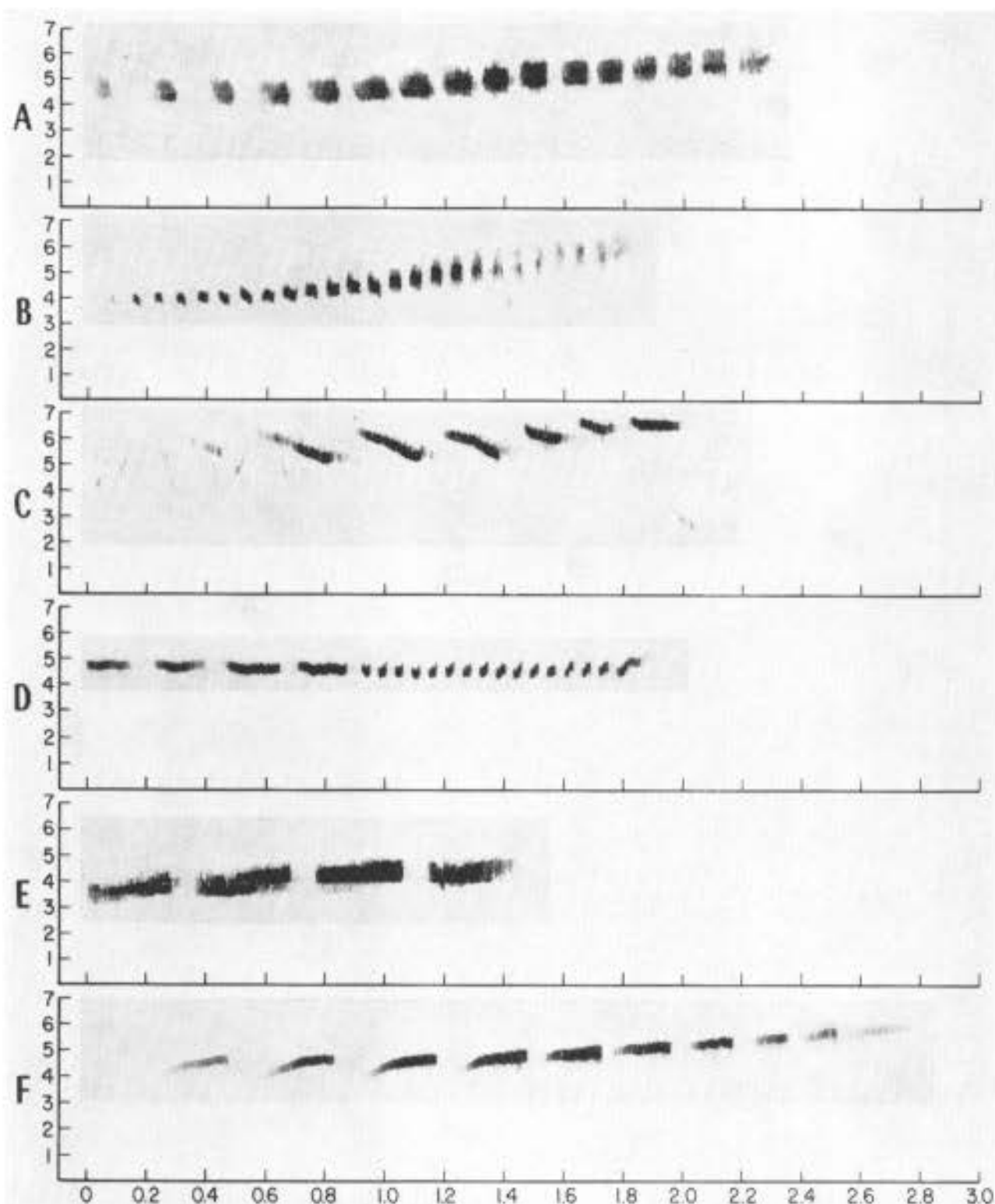


FIGURE 7. Sonograms of Prairie Warbler songs. Numbers on the Y axis indicate frequency in kHz, on the X axis time in seconds. Song A is a Chatter, B a Trill, C a Sing-song; and D, E, and F are group-B songs. Song D sounds much like that of a Field Sparrow. See text. (Recorded by Ellen D. Ketterson.)

enough to measure light intensity at time of first song; I could not take notes without a flashlight and could not see the singers until many minutes later. An exposure meter (General Electric model DW68) turned eastward toward the horizon registered 1 fc between 10 and 15 min after singing began. Figure 8 compares time of first song and time of civil twilight on 27 clear mornings, 23 April–21 July. As shown, first song was a mean 1.3 min (SD 9.8 min) before civil twilight, but the

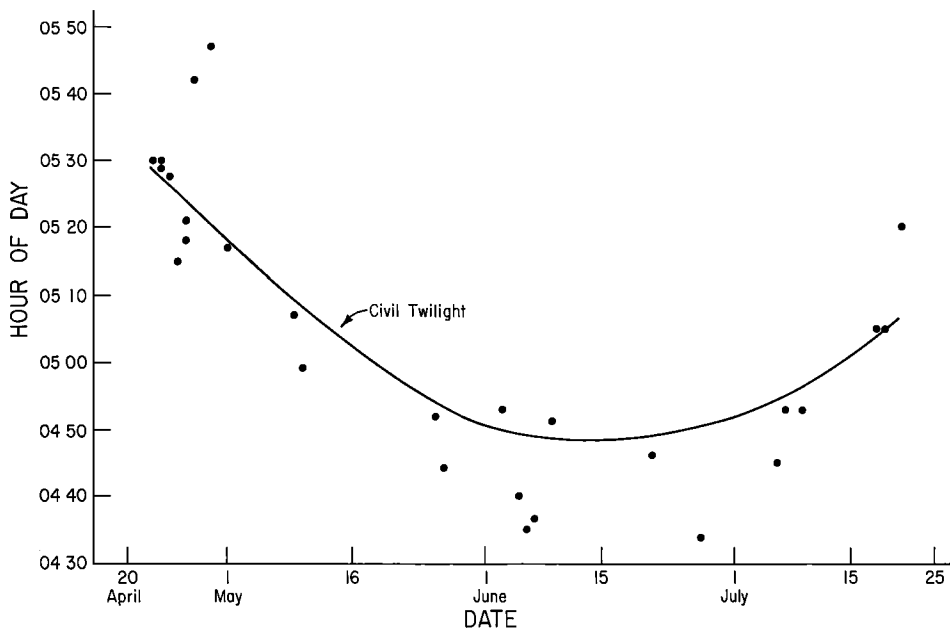


FIGURE 8. Time of first song on 27 clear mornings, 23 April–21 July, relative to time of civil twilight. Time is eastern standard.

data are not normally distributed around a constant mean. Singing became earlier relative to civil twilight until mid-June and then gradually grew later (compare Armstrong 1963: 196). Often two or three males, perhaps mutually stimulated, started to sing within a short span.

Throughout pair formation each male sang his preferred group-A version (p. 68) at dawn, but near the end of building or start of laying in the first nest loud group-B songs gradually replaced group-A. Thereupon males began also to intersperse among their dawn songs the loud Harsh Chek calls often heard in fights (see Chapter 9; compare Nice 1932, Morse 1967). The frequency of these varied considerably among males but seemed fairly constant for each individual. Usually about five songs were given before the first calls; but one male typically called after his first song, and some males sang for several minutes before calling. The initial two or three calls between songs were faint, but within 5 min calls became loud. Songs were usually 10–12 sec apart, and the number of calls between any two songs ordinarily was 12–18 (maximum 64). Calls were irregularly spaced, tending to come in bursts. The period of calling was 25–45 min (mean 30 min) in about 50 recorded cases. Toward its end, calling almost always diminished gradually over several minutes and often stopped 10–15 min before the singing of group-B songs did (at about 0530–0605 in May, 0530–0550 in June). A few minutes later the first group-A songs of the day were given.

I heard dawn calling from 2 May to 18 July, but on 2 May there may have been an actual fight; the first certain case of dawn calling without fighting was on 6 May. Males whose mates were in the egg-laying stage sometimes neither sang nor called

TABLE 11
APPROXIMATE MEAN HOURLY FREQUENCY¹ OF MALE SONG PER QUARTER OF DAY, ACCORDING TO STAGE OF REPRODUCTION

Stage of reproduction	Males observed	Minutes of counting	Mean songs/ hour ²	Minutes of counting	Mean songs/ hour ²	Minutes of counting	Mean songs/ hour ²	Minutes of counting	Mean songs/ hour ²	Mean daily total ¹⁸
		0430–0830 ⁴		0830–1230		1230–1630		1630–2030 ⁴		
Prior to arrival of female ⁵	22	1628	197	792	189	314	174	150	(87)	2304
Attempting to pair ⁶	11	1025	185	361	155	690	116	240	(71)	1852
After pair formation, before nest building ⁷	19	2385	85	966	48	1560	59	540	76	991
Active nest building, ⁸ except final day	27	1396	62	1410	76	1168	70	970	47	965
Active nest building, ⁸ final day	5	720	37	630	4	480	3	730	10	192
Inactive phase of nest building ⁸	15	540	46	570	46	119	(61)	180	10	624
Laying ⁹	16	1412	55	1453	33	720	24	603	22	497
Incubation period ¹⁰	16	4100	115	4331	66	2980	51	2682	52	1052
Nestling interval ¹¹	9	1360	57	4466	44	1180	41	465	29	640
Period of dependence after nest-leaving ¹²	23	885	55	1838	67	1080	71	585	52	926
Immediately preceding building of second-brood nest ¹³	8	105	(31)	750	53	75	(24)	75	(30)	— ¹⁴
Nest building for second brood	4	137	(18)	516	40	165	(133)	110	(113)	— ¹⁴
After loss of female, May–10 July	14	350	174	805	185	165	(207)	220	(178)	— ¹⁴
Totals, all periods		16043	100	18888	66	10696	62	7550	49	

¹ Most counts lasted at least 30 min, a few only 10 min. Only counts in favorable conditions for song are included.

² Means for counts lasting less than 6 hours are in parentheses.

³ Totals are calculated by multiplying mean songs/hour by the number of hours in which it was light enough for males to sing. The first and fourth periods were 3 hours long prior to arrival of the female and while the male was attempting to pair; at other stages these periods lasted 3.5 hours.

⁴ Time before the day's first song and after the last song is not considered.

⁵ Excluded are data from males that had arrived less than 24 hours previously and males that were apparently not fully territorial.

⁶ Included are all observations during which a previously unmated male was associating with, or watching, a female that had appeared on his territory that day.

⁷ Data are taken from the pre-nest-building period of first and replacement nests but do not include the day on which the male and female began their association.

⁸ See page 149 for definitions of the phases of nest building.

⁹ This period excludes the day on which the final egg was laid in a complete set.

¹⁰ This period includes the day on which the final egg was laid in a complete set; it ends with the male's first visit to the nest after an egg hatched.

¹¹ This interval runs from the hatching of egg 1 to leaving the nest by the last young to leave.

¹² Dependence ends with the final separation of parent and fledglings. Data from days just preceding and during the building of a second-brood nest are excluded and shown separately.

¹³ This period runs from the beginning of the female's pre-nest-building behavior to the start of building.

¹⁴ Mean not calculated because data for at least two periods of the day were inadequate.

TABLE 12
AVERAGE FREQUENCY OF SONGS IN MORNING AND AFTERNOON, ACCORDING
TO STAGE OF REPRODUCTION¹

Stage of reproduction	Average songs per half-day		Morning total as % of afternoon total
	Before 1230	After 1230	
Prior to arrival of female	1347	957	141
Attempting to pair	1175	677	174
After pair formation, before nest building	489	502	97
Active nest building, except final day	521	444	117
Active nest building, final day	145	47	309
Inactive phase of nest building	345	279	124
Laying	324	173	187
Incubation period	666	386	173
Nestling interval	375	265	142
Period of dependence after nest-leaving	460	466	99

¹ Average frequencies are derived from data in Table 11. Terms for stages of reproduction are defined in Table 11.

at dawn, but virtually all males called as described during incubation. About half the males sang group-B songs and called in the nestling interval and still fewer did so thereafter.

When weather was rainy males ordinarily omitted calling and singing group-B songs at dawn and began the singing-day with group-A songs.

Those males for which I have information sang group-B songs and called at dawn after losing mates in midseason, unlike males without females in early spring; these latter sang group-A dawn songs.

Males singing at dawn sounded as though they were no higher than 3–4 m and were changing perches after 5–15 songs.

Hourly distribution of song.—Individual males were inconsistent in number of songs sung at any particular time of day. For example, on 17, 24, 28, and 29 May, I counted all songs of a male whose mate was incubating; between 0730 and 0830 on those days he sang, respectively, 169, 73, 128, and 54 songs; in contrast, his daily totals of songs, viz. 1164, 1158, 1589, and 1235, were rather similar. When the day is divided in four 4-hour periods the inconsistency remained.

During incubation and other stages, males sang most during the half-day ending at 1230. Table 11 was prepared from about 900 hours of song counts (no count briefer than 10 min, many males counted) at all hours of the day throughout the nesting season. Songs were tabulated according to quarter-day and stage of reproduction, and the mean hourly frequency for each quarter-day at each stage was calculated. As during incubation, no consistent pattern per quarter-day emerges; but when the data in Table 11 are used to calculate numbers of songs per half-day per stage of reproduction (Table 12), it is evident that song tended to be more frequent in the first half of the day. Further, from one stage to another, the proportion of the day's songs sung in the morning was about the same except on the last day of nest building (see Table 12). On that day the male usually followed the female silently as she gathered material and built (Chapter 16); because she ordinarily did not build much during the early hours, he spent less time with her and accordingly sang more often.

Last songs of day.—Figure 9 compares times of last song and of evening civil

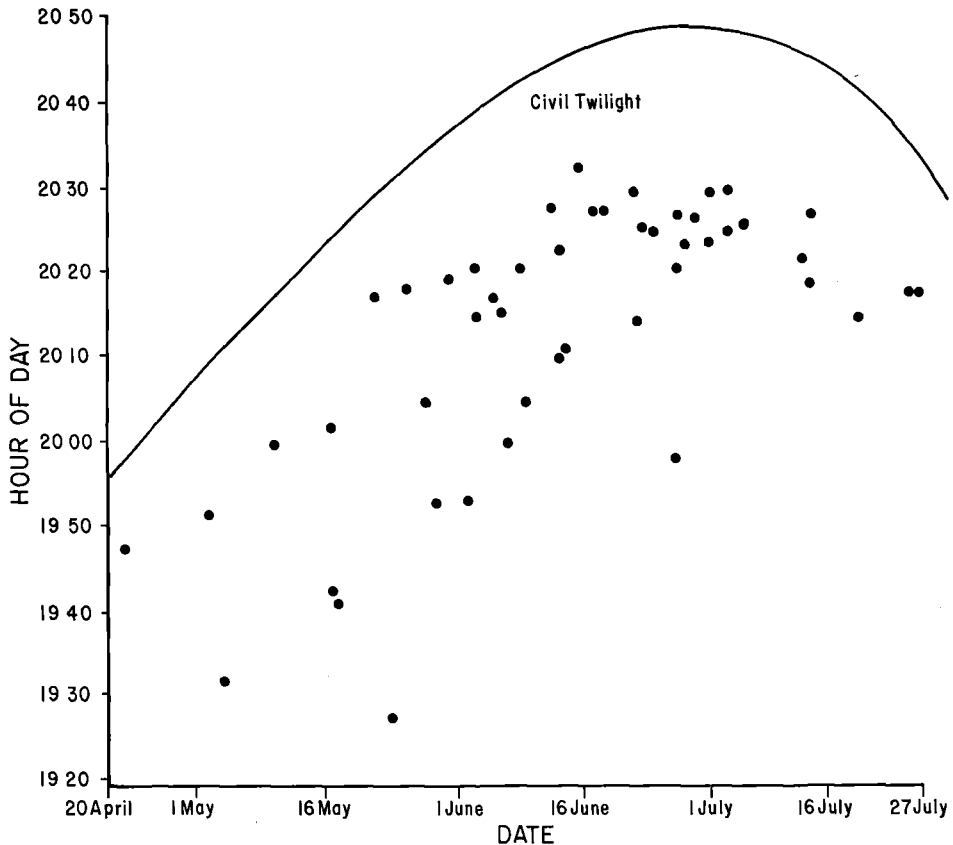


FIGURE 9. Time of final song on 48 clear evenings, 22 April–26 July, relative to time of civil twilight. Time is eastern standard.

twilight on 48 clear evenings. Males stopped singing at higher light values than those at which they began singing at dawn (compare Armstrong 1963: 202). Omitting six cases in which cessation of song was too early to have been associated with changing light, last song preceded civil twilight by a mean of 22.7 min (SD 7.3 min). I measured light at last song on 13 evenings, using an exposure meter directed straight upward. Intensities varied between 4 and 25 fc (mean 9 fc). Cloud cover, rain, wind, and (probably) temperatures lower than 4.4°C all caused singing to stop early; sometimes no singing at all occurred in the hours just before nightfall.

Before and during pair formation, males rarely sang group-B songs. Thereafter versions from either group were sung as the final song of the day. Calling similar to that at dawn also occasionally occurred at dusk but never for more than 3–4 min and never as loud as at dawn.

SONG GROUPS

Methods.—I recorded the group from which some 200 males selected their songs and the circumstances surrounding the singers during all kinds of weather through-

TABLE 13
SELECTION¹ OF SONGS, BY GROUP,² ACCORDING TO ACTIVITY OF MALE
AND STAGE OF REPRODUCTION³

Activity, stage of reproduction	Group-A ² only		Group-B ² only		Groups mixed
	N	% ⁴	N	% ⁴	
Males, not fighting					
Migrating	1	—	1	—	7
Immediately after arriving on territory in spring	44	100	0	—	5
After becoming territorial, before pair formation in spring	105	97	5	3	0
Pre-nest-building period	92	97	3	3	1
Active phase of nest building except final day	111	65	60	35	37
Active phase of nest building, final day	32	65	17	35	3
Inactive phase of nest building	43	60	29	40	4
Laying	58	60	38	40	10
Incubation period	184	74	66	26	—
Nestling interval	76	64	42	36	—
Tending young out of nest	25	61	16	39	12
After midseason disappearance of mate ⁵	47	94	3	6	—
During August and September	12	19	50	81	2
Males, fighting at territory boundaries ⁶	54	18	238	82	20

¹ See pages 65–66 for sources of data. The series of songs immediately following dawn is omitted, as are songs in the final series of the day.

² See page 60.

³ Stages of reproduction are defined in the chapters dealing with these stages, except that the incubation period ends when the first egg hatches. See footnotes to Table 11.

⁴ In calculating percentages, males mixing songs from both groups are disregarded.

⁵ The data are taken from the day following disappearance.

⁶ In addition, 61 males did not sing during fights.

out the season. As will be shown, songs were in series; within a series alternating between groups was uncommon. Table 13 gives the relative frequencies of group-A series, group-B series, and mixed series under various conditions. Excluded are songs at dawn and dusk; all other daylight hours are represented in roughly similar proportions for each condition tabulated.

Results.—The following summary of factors associated with choice of song group includes a few facts not reflected in Table 13.

1. For a brief period, usually a few hours, after arrival on migration group-B songs were sometimes interspersed with the more frequent songs from group A. When males became fully territorial and began to sing steadily, they sang group-A songs almost exclusively except when fighting. This continued until a female was acquired and the pair had been associating for 2 to 3 days.

2. Most males that were engaged in or had just concluded boundary fights sang group-B songs; 77% of the fighters that sang at all sang group-B versions exclusively; 83% sang at least one group-B song. But unmated males fighting in the presence of an unattached female that probably had just come into the vicinity always (10 cases) sang group-A songs. After a male had trespassed deeply into the territory of another and been chased out, the evicting male usually sang group-A songs and the trespasser group-B songs.

3. When nest building began in spring, group-B songs were no longer reserved almost exclusively for fights; during building, 35–40% of all songs were of this group. Trespassing by neighbors during nest building and the aggressiveness this engendered (see pp. 52 and 342) may have caused selection of songs from group B at that stage, but other factors probably also played a role. As evidence, percent-

ages of group-B songs were about the same during building and feeding of young; agonistic motivation appeared to be very low when young were being tended and thus may have been so during building.

4. The relative frequency of group-A songs probably rose during incubation and fell when the eggs hatched. Proportions of group-B during building, tending nestlings, and caring for fledglings were similar.

5. After reproduction males sang little, and the proportion of group-B versions rose to about 80%. Among 29 males heard singing in August, 25 sang group-B songs. Most were in heavy molt.

6. Except that a substantial portion of the day's group-B songs usually was sung at dawn, selection of songs from this group did not vary according to time of day. This statement is based on analysis (not presented) of many day-long counts of all songs of males with incubating and brooding mates.

Many of the foregoing circumstances in which Prairie Warblers tended to select from one or the other song group are strikingly similar to circumstances reported for other wood warblers (Ficken and Ficken 1965, 1967a; Morse 1966, 1967). A distinction between songs associated with fighting and those associated with territorial establishment and advertising for a female is especially clear in the Parulidae (Ficken and Ficken 1962).

Functions of song, according to group.—The foregoing results suggest that group-A songs are specialized for pair formation and pair maintenance and express a dominant sexual motivation. In the absence of sexual stimuli, or when sexual motivation is overridden by strong agonistic tendencies, males tend to sing group-B songs. Group-B songs thus appear to be generalized in function, as suggested by the diversity of situations in which they predominated; very agonistically inclined birds usually selected songs from group B (compare Ficken and Ficken 1965; Morse 1966, 1967), but so did those apparently least agonistically motivated and least motivated to sing at all, such as migrants and molting birds. Note that none of three males that lost mates and thereafter selected most songs from group B gained a new female (but not all males that did sing group-A songs in these circumstances attracted a new female).

It seems clear that group-A songs function to bring males and females together. The high relative and absolute frequencies of these songs during the incubation period (Table 13) suggest that a probable second function is to help maintain the pair bond when the female is alone for long intervals (but note that polygynous bonds most often formed when the male's first mate was incubating; see p. 364).

If group-A songs are more specialized, this suggests they have a later origin than group-B songs. It may be that the Sing-song, the group-A version most like group-B versions, represents the link between the two (see Fig. 7).

Functions of song without regard to group.—(1) Songs of both groups undoubtedly informed neighbors of each other's whereabouts and probably also something of the state of affairs on their territories. (2) Most males with nestlings sang a significantly larger proportion of their songs before arriving at the nest with food than when at a distance from the nest (see pp. 283–284). Song seems to function at this stage in coordinating attentive behavior of the pair and reducing disturbing effects that might be produced by the male's unexpected arrival at the nest (see Chapter 25 for the female's responses to the male's appearance at or near the nest).

If song has this function, its reduced frequency away from the nest would probably enhance its signal value when the male is about to bring food. (3) Song may communicate information to fledgling young, telling them of the father's presence and probably helping him find them (they sometimes responded by calling). It may also encourage fledglings to remain perched where the male left them rather than to expose themselves to predators or to getting lost by seeking him. While the proposed function of conveying information to the young seems plausible, the fact that the female does not sing may cast doubt on the point. The male and female usually took permanent charge of particular young (Chapter 28), and no evidence suggests that the female's wards were at a disadvantage because of her failure to sing.

SELECTION OF SONG VERSIONS WITHIN GROUP A

Size of repertoire.—I had each of 46 males within earshot for at least 50 hours in a season and heard 38 of them (83%) sing all three versions of group A. Four of the remaining eight omitted Sing-song, three omitted Chatter, and one omitted both Sing-song and Chatter. No evidence suggests that old males had larger repertoires than yearlings. Before concluding that some males lacked one or more versions in their repertoire, the following should be considered: A banded male whose mate's nest I watched sang no Sing-songs, until in my 46th hour of watching he sang a series of 26 of them; I heard no others in 10 hours of watching thereafter. A male that in 1956 sang no Chatters during 53 hours sang 80 Chatters during the first 30 hours in which I watched a nest on his territory in 1957.

Preferences.—I concluded that each of 56 individuals had a preferred group-A version. This preference was indicated by (1) its almost exclusive selection during uninterrupted group-A singing before pair formation, (2) its greater frequency compared to the other versions after pair formation (compare Ficken and Ficken 1967a: 159), and (3) its selection as the first group-A song of the day. Distribution of individual preferences was as follows: Chatter, 28 (50%); Trill, 17 (30%); intergrade between Chatter and Trill, 2 (4%); Sing-song, 9 (16%).

Sing-songs became much less common from 1963 on; only one male preferred Sing-songs after that year, and other males sang it very rarely. Possible explanations are that the decrease in the population of the study area (Chapter 38) reduced the chance that the least preferred version would be represented, and (2) selection of a version was often facilitated by a neighbor's singing it, as discussed below. Males that preferred Chatter and Trill rarely heard Sing-song from neighbors and thus were not stimulated to select it.

Thirty banded males whose group-A preferences I knew were present in more than one year, and no change of preference ever occurred. These 30 males represented a total of 83 seasons on the area, and distribution of preferences among them corresponded to that in the population as a whole.

Individual differences in song, some very pronounced, were recognizable and persisted from year to year.

Extent of alternation among versions.—As noted, before acquiring a mate each male steadily repeated his preferred group-A song with rare exceptions (compare Ficken and Ficken 1967a: 159); this was as true of most males that lost mates in

midseason as of newly arrived males in spring. During the first several hours or days of association with a female, the unvarying vocal behavior continued. Thus, a male that showed unusual impartiality among group-A versions after he became paired sang only Trills during my first 33 hours of observing him before he paired. He acquired a female on 29 April, but I heard him sing no Sing-songs or Chatters until 4 May. Again, in my 3-hour watch of another male, he sang only Trills on the day he began a temporary association with a female. Next day he occasionally introduced several Sing-songs and Chatters, and the following day he sang all three versions near this female. She left the territory permanently at 1200 that day; the male sang only 194 Trills while I listened that afternoon. Next day he sang only 424 Trills during 140 min of observation; his mate for the season then appeared. On the following morning he sang 364 Trills and 8 Chatters in about 120 min. Thereafter Chatters and Sing-songs became more numerous.

Interpreting the foregoing information, I assume that Prairie Warblers recognize the voices both of neighbors (see p. 41) and of members of their own families (compare Weeden and Falls 1959, esp. Table 1). That the female recognizes her mate's voice or his songs is supported by many episodes. Females often called immediately following a song by the mate. Seven times while more than one male sang nearby, females called following the songs of their mates but not after those of the other males. Identical behavior was also observed in fledgling young that could hear both their father and other males. Given the probable existence and importance of individual recognition of song, the male's restriction to one preferred group-A version during his early association with a female may have permitted her to become thoroughly familiar with his rendering of his principal song and perhaps familiar with the general characteristics of his voice. Pair formation, including both bond establishment and the female's becoming acquainted with the territory's limits, would be simplified and made more efficient by the male's avoiding variety at this time. When he later introduced his full repertoire, the female presumably learned the individual characteristics of all his performances.

A second possible advantage in continuing to sing one version after the female appeared is connected with the fact that neighboring males, especially if unmated, took an interest in and sometimes interfered with pair formation on adjacent territories (Chapter 7). Immediate change in a male's vocal behavior might notify neighbors of the arrival of the female earlier than they would otherwise learn of it and increase their interference.

Analysis of day-long records of songs by individuals reveals no other tendency to sing particular versions at particular times (except that the preferred version was the first sung after dawn vocalizing ended) or in certain sequences. Similarly, among group-A versions evidence of motivational differences underlying song selection is lacking. Hinde (1958) has proposed that having a repertoire permits a male to direct at each neighbor a vocalization the effectiveness of which is intensified by its resemblance to that neighbor's own song; this view seems to me to presuppose that motivational differences are not primarily responsible for the selection of versions within a group. In support of Hinde, many times one male's singing appeared to facilitate performance of the same version by a neighbor. For example, an individual (male A) I had studied for many hours sang no Sing-songs until a male with that preference took over the adjacent territory, immediately

TABLE 14
NUMBER OF SONGS IN SERIES,¹ ACCORDING TO HOUR OF DAY

	Hour of day					
	Dawn	0600	0830	1230	1630	Dusk
Cases, N	15	35	35	35	35	9
Mean	117	30.2	19.3	18.8	20.3	18
SD	—	28.6	17.3	11.5	17.3	—
Extremes	235-2	123-3	87-4	51-4	67-3	50

¹ See text, this page.

after which male A began frequent Sing-songs. (See also the discussion above of the virtual disappearance of Sing-song after 1963.)

Neighbors singing the same group-B version sometimes seemed to do so antiphonally; they performed alternately for so long that chance could hardly have produced such synchronization. Antiphonal singing in other species is imitative and in some cases is thought to yield the same advantage that Hinde proposes for singing a song like that of a neighbor (Armstrong 1963: 53, 126-127).

SERIES OF SONGS AND THEIR CADENCE

I arbitrarily define as a "series" two or more consecutive songs in which no interval separating the first notes of successive songs exceeds 45 sec. The "cadence" of delivery of a series has been defined by Reynard (1963) as "the average length of time from the first note of a song unit to the first note of the succeeding unit throughout the whole song performance," including the "period . . . in which the song unit is heard and the silent period between song units."

Length of series.—The longest series recorded were two sung at or shortly after dawn. One consisted of 235 Chatters (in 55 min) and one of 189 Chatters (in 54 min). Long series were also sung at other times of day by males whose females were incubating. Examples are 153 Chatters, 136 Sing-songs, and 123 Trills.

To learn if length of series varied as the day advanced, I analyzed counts made during day-long watches in the incubation period, the only stage for which I have adequate data for males unquestionably still in full song. Series at six different times of day were considered. These were (1) all available dawn series of group-B songs; (2-5) the first five series sung by each of seven different males at or next after 0600, 0830, 1230, and 1630 (thus 35 series for each of these times); (6) the final series of the day of all males whose songs were counted throughout the day.

As Table 14 shows, the series at dawn was usually the longest of the day; the mean, 117 songs, was nearly four times greater than the next largest mean, which was at 0600. Length decreased from about 30 at 0600 to about 19 at 0830 and thereafter changed little.

Cadence.—I obtained information about cadence by timing intervals between the first notes of successive songs in a series and also by counting songs in series of known duration and dividing for means.

Variation in cadence within single series.—The following data from single series sung by five perching (not foraging) males are representative; mean intervals and

TABLE 15
SONGS PER MINUTE OF SINGING¹ AND TIME SPENT IN SILENCE BY SELECTED
MALES DURING DAY-LONG WATCHES IN INCUBATION PERIOD

Male	Date	Day of incubation	Time of			Quarter-day			
			First song	Last song		0430-0830	0830-1230	1230-1630	1630-2030
1	24 May	8	0514	1928	songs/min singing ¹	2.3	2.7	2.0	1.9
					total min silence ²	63	60	115	123
2	18 May	1	0525	1941	songs/min singing ¹	3.6	3.5	2.0	1.9
					total min silence ²	152	131	180	151
3	9 June	7	0451	2004	songs/min singing ¹	4.0	3.8	2.5	3.7
					total min silence ²	111	210	171	135
4	10 May	1	0505	2000	songs/min singing ¹	4.7	3.9	3.8	2.9
					total min silence ²	102	170	176	115
5	24 May	2	0444	1900	songs/min singing ¹	4.1	4.4	2.6	2.9
					total min silence ²	153	233	198	— ³

¹ Minutes of singing are those between the first and last song in a series, as defined on page 70.

² Minutes of silence are those between the last song of a series and the first song of the next series, as defined on page 70. Time before the first and after the last song of the day is excluded from the first and last quarter-days.

³ No observer was present during the last hour, and this quarter-day is excluded.

extremes of time between two successive songs are shown in seconds. (1) 26 Trills: mean 13.7 (SD 3.8), extremes 11 and 30. (2) 20 Trills: mean 13.4 (SD 1.8), extremes 10 and 19. (3) 14 Chatters: mean 11.0 (SD 1.5), extremes 8 and 14. (4) 11 Trills and group-B version mixed: mean 14.3 (SD 3.5), extremes 11 and 23. (5) Group-B version: mean 12.7 (SD 4.5), extremes 8 and 23. Males foraging steadily sometimes sang at cadences similar to these, if they encountered no food items difficult to seize or to prepare and swallow; but foraging birds usually sang both less regularly and less often than perching ones.

Variation in cadence among series.—Individual males did not usually sing several series at the same mean cadence, even though the version was the same in all the series. Five series sung by each of four males will illustrate this. Each was composed of at least 20 songs; the versions sung by each male were the same in all series; each male had an incubating mate; all series were sung before 1230. Mean cadence is in seconds. (1) Male singing Trills: 18, 20, 15, 11, 21. (2) Male singing Chatters: 16, 12, 14, 20, 17. (3) Male singing Sing-songs: 20, 21, 24, 17, 19. (4) Male singing group-B version: 13, 9, 18, 10, 22.

A sign test was performed on the mean cadences of matched pairs of series of many males, one series consisting of group-A songs and the other of group-B; each pair was sung by the same male, and all males had incubating mates. The test revealed no difference in cadence associated with group.

Variation in cadence according to time of day.—To learn whether cadence changed as the day advanced, I used data from five day-long watches at nests of males whose mates were incubating. Throughout these days I recorded the times at which each series began and ended as well as the number of songs in the series. The data show no tendency to sing at a faster cadence during any one hour than during the hour immediately preceding or following, or during early as opposed to late morning, or during early as opposed to late afternoon. But cadence was faster before 1230 than afterwards (Table 15). Silent intervals were the same, morning

and afternoon. Thus, the slower afternoon cadence was responsible for the fewer songs sung after 1230 than before (p. 64).

MISCELLANEOUS INFORMATION

Volume.—Volume seemed to vary in a continuous graduation between loud songs and songs so faint that the singer was barely audible from 4–5 m. Singing at less than full intensity sometimes accompanied visible behavior (e.g. concentrated watching of a female or rival male) that suggested tension and excitement. At other times faint songs sounded merely slack, unemphatic and slightly abbreviated, suggesting weak motivation to sing. Occasionally loudly singing males suddenly tensed, began to sing faintly, and seemed to stare at something I could not see. Usually the bill and throat moved less as volume decreased, but I was never certain that a male sang with the bill entirely closed (see Armstrong 1963: 63). The clearest examples of listless, faint songs were those of migrants or of molting males. Less pronounced cases occurred when males carried food to nestlings and fledglings.

Ventriloquism.—At times it was difficult to ascertain the direction from which a song came; some observers (Wetmore and Lincoln 1933: 56, Butler 1931) regard ventriloquism as usual in the Prairie Warbler. Faint, high pitched songs were especially difficult to locate, as expected (see Armstrong 1963: 21–24).

Perches, positions.—Males sang probably during all their activities while perched, except while sunbathing. Thus, to sing they interrupted all other activity. Song in the nest tree was very rare, but one male sang while perched on the nest.

Positions of the body and head varied. Typically the long axis of the body formed an angle about 25° from the horizontal, and the tail usually extended the line of the body. The head was held at a slightly greater angle than the body, and the bill was opened about 5 mm at the tip. Males could and did sing in many other positions, e.g. while turning the head to look over the shoulder or with the body horizontal and the head thrust forward and downward to permit scrutiny of something below.

In sexual chases males often sang in flight (p. 81); songs were also sometimes given in flight during chases of males. Males happening to fly at the moment the cadence called for the next song sometimes sang it. Songs of all versions were given in flight. The head was elevated and thrown back as much as appeared possible, and the back was arched; the wings were extended and appeared to beat in rapid, shallow strokes; the body was at an angle of about 45° above horizontal; flight speed was much reduced.

Influence of weather.—The relationship between weather and the beginning and end of the day's songs is considered above. Light rain had little effect on song unless it was also windy or cold, in which case frequency decreased whether it was raining or not. Persistent rain, especially if heavy, reduced song greatly. For example, a male that sang 522 times on a fair day between 0830 and 1445 sang only 175 times between those hours a few days later on a warm, windless day of almost steady, sometimes heavy, rain. His mate was incubating both days.

High temperatures (to 38°C), mists, and high humidity had no apparent effect.

SONGS OF IMMATURE MALES

I heard immature birds sing on only six occasions during hundreds of hours. One singer whose age I knew was 70 days old. The others were independent, i.e. probably at least 40 days old; the dates were 7 August–7 September, so no bird was older than 90–100 days.

All songs were abbreviated and somewhat toneless and flat (as were many songs of adults in August); all were clearly recognizable as belonging to one of the standard versions. Four birds sang group-B versions and two sang group-A (slow Chatters). One singer appended to some of his very short Chatters three lower notes that are absent from songs of adults. He also ran two and three songs together (at much less than full volume), as a result singing 12 times in 1 min. Another young male sang 10 times in 3 min, then for 10 sec called the Harsh Cheks that are often uttered during fights. The remaining males sang five or fewer times. All were foraging.

SONGS OF FEMALES

I saw female Prairie Warblers sing on seven occasions (compare Huff 1929, Eliot 1933, Reading and Hayes 1933, Ficken and Ficken 1967a: 156), to which might be added four probable cases in which I heard Prairie Warbler-like songs and found females nearby 10–15 sec later. One bird sang in two different years. The four uncertain cases are referred to below only when they might add information beyond that provided by the definite observations.

The songs were diverse. None sounded much like a male's, but five of the seven I would have recognized as Prairie Warbler songs. The notes (2–9) in these five were hoarse and rasping, somewhat the quality of certain male group-B versions. The two unrecognizable songs were squeaky. In one the female with great effort, head thrown back and bill wide open, uttered two short two-syllabled sounds, and the other consisted of three notes. The number of songs ranged from 1 to 12, the 12 distributed over 4 min.

All cases, including the four uncertain ones, occurred between 27 April and 13 May, i.e. at or very shortly after the beginning of breeding. Of the certain cases, three fell on the day that the female appeared on her mate's territory, but one of these females had been on the study area on the two preceding days and another had been present at least the previous day. One each of the other certain cases fell on the 2nd, 3rd, 8th, and 10th day following pair formation. No female had started nest building. In one uncertain case the female did not remain and pair on the study area; in two the birds had begun to build; one female had just laid her final egg. Thus all four uncertain cases occurred at stages for which there is no counterpart among the definite cases.

Females that I saw sing had been foraging normally just beforehand, two accompanied closely by mates. The songs of the female that sang 12 times contained 4–8 notes and sounded like the fragmentary songs sometimes given by males in the excitement of a fight (Chapter 7). The male, which was courting and flying in display before her, did not react visibly to the songs; nor did the other female that sang with her mate elicit any response from him.

In six of the seven certain cases the females were more than 1 year old; the age

of the other was unknown. Three singers had been banded in previous years; two were at least 3 years old, one was at least 4 years. In one uncertain case the female was at least 3 years old. All the females nested as often and at least as successfully as the female population as a whole.

These individuals showed most of the characteristics enumerated by Nice (1943: 127–132) in her discussion of singing by females of species in which ordinarily only the male sings: The songs were simple and possibly primitive; they were given early in the season and only sporadically; the singers whose ages were known were not yearlings and may have been quite old. Armstrong (1963: 175–178) relates female song in species in which it is exceptional to old age, isolation, injection of male hormones, or physiological peculiarity, often endocrine imbalance. The female Prairie Warblers were in no way male-like in other behavior, with one possible exception: All three females that I saw sing and that were banded had shown site fidelity by returning to the study area, a characteristic uncommon in female Prairie Warblers (Chapter 37).

CHAPTER 9

CALLS

CALLS OF ADULTS

On the basis of differences in sound or context or both, I identified 10 calls (summarized in Table 16). No electronic analysis was made. Males gave all calls, and females were heard to give eight.

Chek.—Variation sometimes made this call sound like *chik* and *chyook*. *Chek* was the most frequent call of both sexes, impossible to classify by context, and apparently uttered in situations producing mild conflict in motivation, alertness, or "curiosity." A few examples of use by males follow: while foraging shortly after ending migration; after reproduction until fall migration, both when isolated and when in mixed warbler flocks; during various kinds of fights; in the presence of snakes, Screech Owls, Blue Jays; when carrying food to nestlings and fledglings. Females used *Chek*, for example, upon coming on a territory in spring and approaching the singing male; just after leaving the nest during incubation; during boundary encounters between males; while soliciting copulation and after copulation.

The variety of situations in which *Chek* was uttered suggests a complex set of motivating states, including a mild aggressive tendency, fear, and sexual arousal. The import of the signal to other Prairie Warblers in some cases was probably to stimulate avoidance or caution, in others simply to reveal the caller's location.

Squeak.—A burst of loud jerky *Chek* calls, but shrill, high-pitched, and squeaky, sometimes was repeated several times in rapid succession and sometimes was followed by fragments of group-B song (see *Whine*, below). The call was most often given during rapid action in intense forms of boundary fighting and after sudden attacks, frequently when the caller was flying in retreat. Both males, including the dominating attacker, seemed to *Squeak* in some fights. Females too *Squeaked* in their rare fights (e.g. in melees) and sometimes when driving small birds from the vicinity of the nest.

Squeaking accompanied very intense agonistic stimulation. Circumstances often suggested the caller experienced fear. As a signal, *Squeaking* may have tended to repel an antagonist; but early in the season, when females were not yet incubating, *Squeaking* by fighting males almost invariably caused females to approach the fight and to call.

Whine.—This loud high-pitched trill had a plaintive, whinnying sound and resembled *Squeaking*. Its quality reminded me of a common group-B song version, and the call often suddenly changed into or was terminated by a fragment of that version. It was given by males flying to repel trespassers, sometimes by escaping males, once during a sexual chase of a female.

Whining may have been intermediate between a group-B song and a call, suggesting the origin of the song. Evidently it was usually associated with predominance of an aggressive tendency and possibly had a repelling effect.

TABLE 16
CALLS OF ADULTS, THEIR CONTEXTS AND PROBABLE FUNCTIONS

Call	Usual context	Usual probable function
Chek	Situations apparently causing conflict in motivations	Indicates caller's location, produces alertness
Squeak	Intense fights	Causes avoidance of caller
Whine	Fights, in flight	Causes avoidance of caller
Harsh Chek	Situations producing aggressiveness	Indicates caller's location
Rattle	Very intense fights, in flight	Repels
Tsip	Alarm, especially toward predator	Produces cryptic behavior in fledglings, alertness and avoidance in adults
Sputter	Sudden intense alarm	Causes avoidance of source of alarm
Squawk	Intense surprise, fear accompanying physical contact	Causes avoidance of source of alarm
Seep	Flight, sudden proximity of mate	Causes following, suppresses aggressiveness and avoidance
Twitter	Close approach to mate or young	Suppresses aggressiveness and avoidance

Harsh Chek.—This derivative of Chek usually was given in bursts of single very loud, coarse, resonant notes; sometimes it sounded like *chenk* or *tenk*. At maximum volume, the resonant and vibrant character may have been responsible for the call's acquiring a second syllable, *che-tenk* (first syllable unaccented). The call was heard in intense boundary fights, but less frequently than Squeak, and probably was associated with a predominating attack tendency. It was occasionally given in flight by victorious males returning from chasing a trespasser, and at times was uttered by males when very close to and displaying toward mates. Its common use during dawn singing is described in Chapter 8. Throughout breeding (58 cases) at all daylight hours it was sometimes given by isolated males, usually at their territory boundaries and at times for many minutes. Females attacking other Prairie Warblers sometimes gave this call.

Harsh Chek is linked with a strong aggressive tendency and must tend to cause avoidance by Prairie Warblers that hear it.

Rattle.—At the greatest intensity of fighting, possibly always while in rapid motion, males at times called a loud vibrant *churr*, *churr*, *churr*. This call followed Harsh Cheks and may have derived from them.

Tsip.—A light *tsip* or *tsu* accompanied alarm (toward predators, humans) and was at times uttered during fights (usually by the attacker) and trespasses. The call caused fledglings and sometimes nestlings to fall silent instantly; while it continued, fledglings remained silent 45–90 min.

Tsip was evidently associated with the tendency to flee. Its significance as a signal to the young is especially clear. To adults it may have had about the same informational content, possibly also functioning to reduce aggressiveness.

Sputter.—Sputtering or twittering resulted from a rapid burst of Tsips and was given in the same situations but apparently when the element of surprise was strong. Typical contexts were experiencing unexpected attack, returning

to the nest and finding me there, hearing a fledgling call in fear. The call probably signaled to other Prairie Warblers the presence of danger.

Squawk.—Both sexes Squawked in states of intense surprise and/or fright and/or aggressiveness, possibly only when subjected to physical contact with an attacking conspecific or predator. Birds sometimes Squawked when I caught them.

Seep.—This high, usually faint, sometimes slightly prolonged note, *seep* or *seet*, sometimes was indistinguishable from Tsip. Usually the call was given only once. It was heard frequently, most often just before or during flight (by migrants, males crossing their territories, parents flying with food for fledglings). Seep was also a close-range communication note between members of the pair (during and after sexual chases, while foraging together, when suddenly coming together at the nest or elsewhere). Some females called Seep after hearing mates sing, and three did so just before or during copulation. Solitary birds foraging after the breeding season occasionally called Seep.

This sound appears associated with social and gregarious tendencies and at times with sexual motivation. The effect on the hearer appeared to be to suppress aggressiveness and avoidance and sometimes to induce following.

Twitter.—This was a rapid burst of Seeps and was indistinguishable from Sputter except that it usually was very faint, audible to me only within 10 m of the caller. Early in their association when a pair suddenly came close to each other, one or both gave the call, as did parents that arrived simultaneously at the nest with food. It was also given (rarely) by an adult when it suddenly approached a full-grown fledgling. In apparently great excitement, perched males sometimes called Twitter while fixedly watching objects that I could not see. The call appeared to be a very intense expression of the tendencies responsible for Seep.

CALLS OF YOUNG BIRDS

This section reports information about the probable ontogeny of some of the calls described above. No young were hand raised, but individuals of every age up to 12 days were taken home and studied for a few hours at a time. Table 17 presents a list of the calls heard, their apparent contexts, and the ages at which they were given.

Chek.—Twice birds about 30 min old, as yet unfed, uttered high squeaks or *cheeps* inaudible to me beyond 2 m. This call, unchanged through the fifth day of life, was most frequent during gaping. At age 6 days the squeak call began to sound like *chip*, by age 8 days it was nearly as sharp and loud as the adult Chek, and beyond the age of 12 days I could not distinguish between the calls of young and adults.

Neonatal birds were silent when prodded and jarred, and did not respond to noises; their first squeaks were probably stimulated by hunger. By age 7 days nestlings apparently had become conditioned to the jarring of the nest as their parents landed, and my jarring also sometimes elicited calling. Until age 10 days, hunger was the only apparent motivation for the call, but at that age a fledgling gave Chek calls during and after a change of perches, seeming to call because

TABLE 17
CALLS OF YOUNG PRAIRIE WARBLERS AND THEIR CONTEXTS, ACCORDING
TO AGE AT APPEARANCE

Call	Age at appearance	Apparent early eliciting stimuli	Apparent later eliciting stimuli
Chek	30 min	Hunger	Change of perch, moderate hunger, surprise, presence of other Prairie Warblers, curiosity
Harsh Chek-rattle	6-7 days	Hunger	Hunger, change of perch, agonistic tendency (?)
Squawk	6 days	Surprise, fear	Surprise, fear
Sputter	8 days	Fear	—
Seep	4 (?)–12 days	?	Flight, presence of adult with or without food, association with broodmates or other Prairie Warblers

excited. Cheks continued to be uttered by fledglings when alone and when they saw or heard a parent. A 13-day-old gave Chek when startled by my approach, and another did so at the approach of a brood mate.

The Chek of birds about 40 days old and older was probably given in the same situations in which adults gave it after their breeding season ended.

Begging call.—The Harsh Chek and Rattle calls of very aggressive males and the sounds of very hungry begging young were often indistinguishable, but because of the difference in the contexts of these sounds at the two ages I have given the call of the young a distinct name. There may be no difference in the sounds of adult and young; recurrence of infantile behavior in new contexts later in life is well known. The only evident link between Begging Call and Harsh Chek and Rattle of males is the apparent high stimulation of the callers.

The earliest form of what may have been Begging Call was heard in birds 6 days old that uttered a two-note high, thin *pip-tsip* when very hungry. By age 8 days Begging Call was common as a burst of vibrant sound, *churr*, very like the Rattle.

After the young left the nest the call changed slightly, was less vibrant, louder and harsher, and except at the moment of feeding less a continuous burst of sound. Component notes could now be distinguished as *tenk* or, when very loud, *che-tunk*, with the last syllable accented as in the adult Harsh Chek. The rate was one or two per second until the parent brought food, when calling became continuous. The vibrant quality of the call after nest-leaving sometimes made it sound both ventriloqual and as though it emanated from more than one bird. It became less common as young grew increasingly able to procure their own food, but sight or sound of the parent stimulated the calling at times, at least until age 41 days.

The call was heard occasionally in situations not obviously associated with begging, e.g. (ages 10–31 days) during a change of perch and during foraging (male, age 44 days).

Squawk.—At 6 days a few nestlings when handled Squawked like adults, and by age 7 days many did so. Nest mates immediately fell silent or, if older, jumped from the nest; and adults approached and began distraction display. Jostling of

young out of the nest and releasing them to freedom also caused them to Squawk, as did surprising events (e.g. the sudden flushing of a Bobwhite nearby).

Seep.—Faint *seeps* were often uttered by birds 4 (once) to 45 days old; the callers never showed the alarm associated with Tsip in adults, and the calls were probably Seep. By age 12 days Seep was associated with flight, as in adults, but also was occasionally given by a fledgling when fed or when it spied a parent. When the young began to move about together (Chapter 28) Seep became common; birds age 40 days and older gave it when they suddenly approached each other and when they foraged.

Thus at least from the time of leaving the nest, Seep was in all significant ways the same call as that given by adults.

Sputter.—Twice calls that sounded like the adult Sputter were given in the kind of context that evoked this call from adults: broods of 8-day-olds that I held in a sack preparatory to banding them gave bursts of faint, rapid, twittering notes.

CHAPTER 10

BEHAVIOR DURING PAIR FORMATION

BEHAVIOR OF NEWLY ARRIVED FEMALES

When not associating with males, newly arrived females usually moved rather slowly, deliberately and silently, seldom foraging higher than 3 m. Progress was by short flights and hops; ordinarily an individual could be followed with ease for several minutes or more. Females seemed excited when on the territories of males that were courting them as well as shortly after leaving those territories; they moved rapidly and somewhat dartingly and called Chek from time to time.

FIRST MEETING OF MALE AND FEMALE

Behavior of males and females varied at first meeting. In about 25 observances of probable first meetings (long watching the male or female before the meeting had established that the bird was alone), the female approached the male and was chased. More specifically, while the male sang out of her sight the female began to move toward the point from which he was audible, changing her course whenever he moved; at times this approach began from a point off his territory. Her progress was silent, low, deliberate, and often interrupted by foraging; flights were 1–20 m long. When within some 30 m of the male, she perched quietly for about 30 sec before flying into the lower part of the tree in which he was singing or into a nearby tree. Her behavior then became alert, her body horizontal and her tail bobbing little or not at all; readiness for flight was evident. She began to ascend, moving 1–3 m and pausing between each move.

The male's behavior did not change during the initial part of the female's approach; it was impossible to know when he spied her. At some point, sometimes when the female was only 2 m away, the male suddenly flew at her and chased her rapidly (compare Kendigh 1945, Lawrence 1953a: 53). Details of this sexual chase are given below; at times the female was caught, and at times she evaded the pursuer.

Some females did not approach the male closely and passed through the territory after pausing briefly, at times to watch the male. The male continued to sing, and but for the fact that he usually followed the female at a distance as she departed, nothing indicated he had seen her. However, one male chased and overtook the departing female and drove her to the ground.

Behavior quite different from the foregoing occurred at five or six meetings. As soon as the female came into view the male performed a slow display flight away from her or at an angle from her. Such flights are characteristic of courtship (see below).

Interpretation of the two divergent kinds of male behavior in meetings with females may be assisted by considering his behavior toward passing, evidently migrating, males. Such birds often behaved much like females and elicited some of

the same reactions. If they did not approach the singer they usually were not challenged and moved off the territory unmolested. If they did approach they were watched, then chased. Most pursued males left the territory, often rising and flying much higher than females normally fly. If they evaded the pursuer and remained, he usually chased them again. After such chasing, the owner did not behave as at the end of sexual chases (below), which suggests that the pursued bird's behavior had caused it to be "recognized" as not a potential mate. No nonterritorial male ever elicited a slow display flight away from him, i.e. the alternate and less common male response to females.

Considering all of the evidence, it is impossible to tell whether males (1) immediately "recognized" females as such and sometimes treated them aggressively, sometimes responded to them sexually, or (2) treated all Prairie Warblers approaching slowly and near the ground as males, leaving it to the newcomers to react appropriately to their sex and internal state.

Ficken (1963) states that female American Redstarts usually approach males gradually and are most often chased immediately. They react by flying downward and remaining on the territory, whereas males that are chased fly horizontally and leave. Although there is evidence that males can and do discriminate between the sexes on sight, they "initially react aggressively towards females . . . , much as they would to intruding males."

COURTSHIP AFTER INITIAL MEETING

Until egg laying, it was impossible to be confident that an associating male and female would form a pair and breed. Associations of several days' duration sometimes suddenly ended, and at least three females deserted males after having begun to build nests. Further, no behavior characteristic of the day of meeting or the next few days was then abruptly eliminated; and activities normally seen only at a later stage of reproduction, e.g. gathering nest material, were sometimes seen on the day of meeting. This section, based on about 200 observations during the early days of the pair's association, describes behavior characteristic of that stage and omits acts usually not seen until later stages of reproduction. Quantitative statements apply only to pairs formed at the beginning of the season (defined p. 89).

Sexual Chase.—Before the chase, the male usually was higher than the female, watching her silently and alertly, sometimes tensely crouching. Rarely he sang very softly, occasionally Twittered.

Suddenly he swooped on the female, either in normal or display flight; the latter was more common if several chases had already occurred. Males often glided down at females with wings extended and scarcely beating. A common variation was fast normal flight until 2–3 m away from the female, then a switch to exaggerated slow butterfly flight or gliding. Another was flight not at the female but at a point near her, then a sudden turn and flight directly at her. Of 95 sexual chases in which males sang (usually a fragment of group A), only once was song given during the approach phase.

The female's response during the first 1–2 days after joining the male almost always was to fly from him when he was quite near; some females turned and faced the male in the tense crouch, darting away just before contact. The male's

frequent slowing of flight when he neared the female gave her a chance to escape, but when she started to fly he then clearly tried to catch her.

The chase was almost always 1–2 m above the ground, covering 5–50 m (mean 20–25 m); the course was irregular. Sometimes one or both birds Twittered; a song or fragment of song was occasionally (six cases) uttered during this phase.

Of 224 recorded chases, 65 ended out of my sight. Of the rest, the male caught the female in 108 and she evaded him in 51. Males caught females by overtaking them and driving them to the ground or by following them to a perch. In 77 catches, females landed on the ground, in 31 in a tree or shrub near the ground. Probably in most catches in which the female flew into a tree, the male had overtaken her in flight and seized and hung on to her tail and compelled her to alight. If she was driven to the ground or alit on a perch before being caught, usually he then seized one or more rectrices (compare Ficken 1963), sometimes at the base, sometimes distally. Tail pulling was vigorous and lasted 1–6 sec; at least once a feather was pulled out. The male jerked his head and if on the ground backed up and tugged; if the female had alit in a tree, he sometimes hung below her fluttering his wings and pulling. In 34 or more cases the male sang (usually one loud group-A song) while pulling the tail; in at least 9 others he sang after letting go. One male let go, retreated 15 cm, spread his tail and drooped his wings, then sang while facing the female; three males behaved similarly but spread their wings as they sang. In other cases of singing after catching, the singer was not clearly visible.

Generally the female tolerated tail pulling for 1–2 sec, facing away from the male and sometimes fluttering her wings. On the ground some tried to escape by hopping, at times beating their wings strongly; one female dragged a male 1 m. After enduring tail pulling briefly many females turned on and repulsed males by thrusts of the bill; a few lunged persistently and forced males to retreat. Three females flew at males and chased them out of sight, the males flying in exaggerated, slow butterfly flight and the females pursuing in less marked butterfly flight.

Not all females let their tails be pulled; especially if driven to the ground, some turned on the male and prevented him from grabbing the tail. The behavior that then followed was exactly the same as that to be described below as “pouncing.”

Whether he pulled her tail or not, the male almost always flew from the female in butterfly or moth flight or glide, or a combination of these. At least four males sang, and an occasional one opened the bill and gaped in flight. After these flights, which usually covered 10–15 m, males almost always perched; but some (18) that had caught the female in a tree glided to the ground instead of to a perch.

In 51 instances, the female evaded the male after flights of 5–75 m. Especially if the chase had been short, the male gave up his fast pursuit, usually performed glide or moth flight, and veered off to perch. At the approximate moment of veering, 15 males sang.

After at least half the chases in which the female was caught and almost all in which she was not, the male perched like a bird that had just concluded a fight, tensely crouching, wings out (rarely drooped), gaping wide with head forward and probably at times with retracted neck. The pose was maintained as long as 90

sec during which the female, if in sight, was watched. In cases of gradual resumption of the normal perching position, closing the bill was probably the last act in the return to normal.

Females that had been caught almost always sat quietly for 10–90 sec after males left them. Subsequent acts varied among displaying (flight-to-male was common, as described below), preening and scratching, shaking the plumage, foraging, carrying nest material, and leaving the territory.

Sexual chases were observed 192 times between birds that remained together and bred, 32 times between temporary associates; numbers are approximate because most females were unbanded early in the season. Of chases between eventual pairs, 101 took place on the first day of association (e.g. 7 chases between the first meeting at 0629 and 0804), 29 on the second day, 8 on the third. The remainder (54) were distributed as follows: from the fourth day until the beginning of building the first nest, 28 (this period lasted several days, as described in Chapter 13); during building of the first nest, 15; during incubation, 1; during preliminaries to building replacement and second-brood nests, 5; during building of later nests, 5.

Sexual chases were observed at all hours until 1915; but of 224 recorded times, about 75% were evenly distributed during daylight hours before 1230; in a test of whether this distribution was random with respect to my time in the field, $P \approx 0.001$. (Most first meetings between males and females were in the morning.)

To learn whether catching the female might be associated with permanence of the pair's association, I considered 99 sexual chases whose outcome I could observe; only those in the first 3 days of association were included. Of 72 chases between birds that did pair, males overtook females in 56 (78%); of 27 chases between birds that did not pair, males caught females in 10 (37%); adj. Chi-square = 12.9, $df = 1$, $P < 0.001$. Among pairs, the rate of success in catching the female did not change significantly after the first 3 days of association (70% catches in 60 chases from the fourth day onward).

The female's evasion and refusal to alight, not the male's lack of effort, usually appeared responsible when the chase did not end in catching. If so, temporary associations probably were attributable to the female's unreadiness to pair or to her rejection of the male. Sexual chasing may be indispensable to pair formation (see Ficken 1963). One male with an injured wing was unable to fly well and could not chase a female that landed beside him. He gave the wing waving display (below) and seemed to walk toward the female, but she immediately left the territory. He sang for another week but acquired no mate.

Display flight.—Independently of sexual chasing, butterfly flight and (most commonly) moth flight and glide (once undulating flight) were performed by the male from the moment of the female's arrival. Flights were low and short, rarely as long as 20 m. Frequently a male took flight in butterfly flight, changed to moth flight and sang a loud group-A song, then glided to a perch. Flights were directly away from the female from a point near her, or toward a point 5–10 m to her side followed immediately by a second flight away from her, or past her to a perch 10–15 m beyond. These flights were conspicuous, at about the female's eye level, but not directly at her.

Display flights were more frequent than sexual chases, with which they were usually interspersed. They were commonest early in the pair's association, de-

creasing as sexual chases decreased as nesting proceeded. However, whereas sexual chases were uncommon after the first nest was built, display flying usually recurred during the preliminaries to building subsequent nests.

Males that courted an unresponsive female often continued to display for some minutes after the female left the territory. Males watching females on adjacent territories sometimes displayed.

Flight-to-male: following by female.—After some 10% of sexual chases and a smaller proportion of display flights, the female flew (2 m high or less) directly at the perched male; sometimes she did so even when he had not displayed recently. This flight-to-male almost always stimulated the male to perform a display flight, which in turn often led to another flight-to-male. As a result, the female followed the male around and across the territory. Flight of the female was slow and occasionally approximated butterfly flight. The distance covered was variable and was sometimes the full width of the territory. Nearly all flights ended with the male's leaving his perch as the female approached and the female's landing on it; note that this occurred also in supplanting attack between males (p. 48). Rarely the female followed the male instead of landing on his vacated perch. When he flew from the female, the male traveled 10–20 m, then alit and watched her. If she did not fly at him again the male often turned and either chased her or flew past her in display; the latter at times caused a new flight-to-male.

Females usually called one or two Cheks, less often Seeps, before flying or after landing. Males generally sang loud, frequent group-A songs while perched; both birds sometimes Twittered when near each other. Flight-to-male was distributed over the reproductive cycle in about the same relative frequency as sexual chases but was two or three times more common; at least 66% took place during the first 2 days of association.

Occasionally a male did not see the female coming and in evident surprise reacted hostilely; e.g. one bowed his head up and down, then gaped with head forward. Sometimes a male started the approach phase of a sexual chase just as the female began a flight-to-male; the female either turned and fled, or the two met in a flutter-up.

Female American Redstarts frequently perform a display that seems much like the one just described (Ficken 1963).

Pounce-on-female.—Pounce-on-female began as a sexual chase but was interrupted because the female did not fly away; it was much more common a few days after first meeting than at the beginning of the pair's association. On 141 male approaches for a sexual chase during the first 2 days of association, the female refused to fly 11 times (8%). On 48 approaches from the third day to the start of nest building, the female refused to fly 19 times (40%); $P < 0.001$. Either of two things happened when the female did not fly. Rarely, she permitted the male to pull her tail when she perched, but usually she reacted aggressively (compare Baird 1967) in one of the following ways: In the least intense and commonest reaction, the female perched motionless, facing the male, her plumage somewhat sleeked, apparently balanced between escape and attack. Some females tensely crouched facing the male with bill pointed about 45° upward (unless the males were below them). Such head-up displays are a common avian threat (Hinde 1964a) but are rarely seen in parulids (see Baird 1967). Occasionally

a female gaped while tensely crouched, her head forward (compare Baird 1967). In the most intense reaction (eight cases), females pecked at males, sometimes darting toward them to do so. Bill snapping was heard once.

Male responses to the foregoing female aggressive behavior can also be graded according to increasing intensity. No response was specific to a particular level of female aggressiveness: (1) Some males flew past the nonretreating female or turned and retreated. (2) Some perched beside or hovered by the female, sang a loud group-A song or fragment, then flew away. (3) Some alit, faced the female in a tense crouch, then flew away. One male and female faced each other tensely for 3 min, 2 m apart. (4) Some males while crouching gaped with head forward. One moved the head from side to side while gaping, and the shining pink lining of his mouth was conspicuous. Another male, finding the female facing him, hopped back and tried to approach her from a different angle; but she kept turning to face him, and he retreated. Females usually did not fly when males gaped, and males soon retreated.

(5) Sometimes a male alit close to the female, faced her, and spread his wings; the spread varied from 50% to full extension, and the angle varied from horizontal to nearly vertical. Rapid quivering of the wings often occurred, termed here "wing waving" following Ficken (1963). In rare variants of this quivering the wings were extended above the back and moved only slightly or raised full length over the back and then beaten deeply and I believe asynchronously (compare Ficken 1963). Some males tensely crouched, head stretched far toward females, bill open; one male sang once. Depending in part on the female's behavior, the male sometimes moved toward her, sometimes away. Short movements toward her appeared to be by walking or sidling, the feet moving alternately. One male without moving his feet toppled backward and hung 1 sec upside down while waving his wings, then flew away, shook himself, and puffed. Once a female pecked at the displaying male, and he returned the peck; the birds hovered together somewhat as in flutter-up. These male-female encounters usually ended in the male's withdrawal. Wing waving is of special interest because it was not given in male-male encounters (see the exceptional cases, p. 56) and may not be derived from intention movements of attack or escape. Ficken (1963: 310) states that wing waving of male American Redstarts is "confined to courtship displays, probably indicat[ing] a strong sexual tendency and [possibly] derived from the balancing movements of copulation" (see also Lawrence 1953b, Ficken and Ficken 1962, Baird 1967).

(6) To wing waving was occasionally added tail spreading (maximum, 9 cm at the tip). At maximum spread a male cocked the tail to 45°, hopped jerkily several times, then quickly fanned the tail open and shut. Slight tail movements may be flight-intention movements; wide fanning and cocking suggest derivation from copulatory behavior (see Ficken 1963, Baird 1967). (7) Many times a male overrode the resistance of a female or reached her before she could crouch and face him. She then flew and the two hovered together or fluttered to the ground. Once a female appeared to be lying on her back, but usually when on the ground females behaved as in sexual chases that ended there, except that there was no tail pulling. Males flew away as when leaving a sexual chase (p. 82).

Behavior related to nest building.—Males sometimes performed nest shaping as

early as the first day of association, and females occasionally picked up nest material or explored for sites. This behavior is described in Chapter 12.

DISCUSSION OF COURTSHIP BEHAVIOR

The dominance of aggressive motivation in males at and just after the time females joined them seems obvious. Some slight escape tendency is perhaps indicated by the delay in starting to chase an approaching female, and escape motivation prevailed temporarily in males that fled from resisting females. The presence of sexual motivation even in highly aggressive males may be indicated by wing waving, since that display was absent in male-male encounters. Also nest shaping, though rare early in the association, appears unrelated to agonistic motivation and may have expressed the sexual tendency.

A paramount escape tendency in the female during the first hours of pair formation was the complement of the male's aggressiveness, but her capacity for aggressive motivation is evident in her resistance to excessive tail pulling. Female behavior clearly derived from or identifiable as an expression of sexual motivation was not apparent at this stage, except for occasional manipulation of nesting materials and visiting of potential nest sites. However, Marler (1956: 96) has said that it might be argued that the attraction which the male has for a female that enters his territory and approaches him is a sexual one.

Sexual chases probably function to dissipate male aggressiveness toward the female, his ritualized victories over her gradually diminishing his hostility and permitting him to tolerate her presence. The extent of that hostility and the rate of its dissipation are suggested by the many chases during their first 1 or 2 hours together and the rapid diminution thereafter. Sexual chases probably also ultimately stimulate the female to become aggressive enough to resist and assert herself, surely a necessary condition before the nest can be built and copulation take place. Flight-to-male and the male's display flights in retreat evidently are a ritualized reversal of the initial relation in which the male is the attacker; presumably this ritual is a mechanism contributing to equalization of the two pair members. The fact that flight-to-male often followed the sexual chase appears significant.

By the time the female was actively exploring for nest sites, the relations of the pair had so shifted that the male was no longer dominant. His approaches and swoops put the female to flight less and less often, and it became usual for her to turn on him and force his retreat. A comparable process of parallel change in courtship behavior and dominance relations has been analyzed in detail for the Great Tit by Marler (1956). In the Prairie Warbler, however, there was no complete inversion; the female never reached the stage of dominating the male.

OTHER BEHAVIOR DURING PAIR FORMATION

A male sometimes appeared to head off a female starting to leave his territory; if she left he might go after her and cause her to return. Thus, females 50–60 m into adjoining territories were sometimes pursued by males and returned immediately.

TABLE 18
FREQUENCY OF TEMPORARY ASSOCIATIONS OF MALES AND FEMALES
AT BEGINNING OF SEASON

Number of female associates before mate acquired	Males	
	N	%
0	54	59
1	22	24
2	10	11
3	4	4
4	1	1

The pair kept visual and/or vocal contact with each other most of the time while foraging and loafing. Neither sex was exclusively responsible for this, but the male probably followed the female most of the time.

Females usually appeared excited during the first days after pairing; they called Chek and Seep frequently (compare Ficken 1963), moved rapidly, and sometimes flew suddenly. They also bobbed the tail more often than at later stages, possibly as a recognition signal or behavior making them more conspicuous to the male (see Chapter 40; Mayfield 1960: 66). When a newly arrived female behaved in this excited way, it usually was safe to predict that a pair would form; absence of excitement was a fairly reliable indication a female would not stay on the territory.

Females, before they began to nest, regularly attended male boundary fights; thus both fighters' mates were present 10–15 m on their respective sides of the boundary. They called loud Cheks, foraged, and followed the fighters as they moved. This sometimes led to melees (Chapter 7). The excitement of boundary fights may have solidified the pair bond and/or acquainted females with territory lines.

MOVEMENTS BY FEMALES BETWEEN ARRIVAL AND PAIRING

Temporary male-female associations.—Inspections at least once daily of 89 territories at the beginning of the season yielded information about the numbers of females that various males courted before obtaining a mate. Observed numbers are minima; many brief courtships probably were unobserved. Another limitation on the accuracy of the data is caused by the fact that few females were banded when they arrived.

Most males were seen to associate only with the eventual mate (Table 18); at the other extreme one male had four temporary associates before pairing. Males that paired without observed temporary associations acquired mates on the mean date 30 April–1 May; the mean for all other males was 5 May. I aged most females that eventually paired with the males in these two groups. Among the mates of males that had no observed temporary associates were 8 yearlings and 41 older females; among the mates of the other males were 14 yearling females and 18 older females. In a test of independence, adj. Chi-square = 6.0; $df = 1$; $P < 0.025$. The greater proportion of yearlings in the latter group is probably attributable to the later arrival dates of females of this age (Chapter 3).

Individuals that arrived already banded provided information about the promptness with which females joined eventual mates, but such females that showed attachment to the study area were in a minority and their behavior may not have been representative. Further, probably not every banded female was seen within a few hours of her appearance.

Females that selected a mate promptly.—Most cases (26, or 70%) tend to prove that pair bonds usually were established very quickly, probably within a few hours of the female's arrival. Counting an individual once for each year she was present, in 21 instances females at least 2 years old were first seen associating with the males that became their mates; so far as known, all these restricted their movements to their mates' territories until nesting began. Four yearlings banded as nestlings behaved in the same way. Another female, which was observed only on her eventual home range, was not seen to associate with the male there on her first day present, although he was her last year's mate and became her current mate.

Females that did not select mates promptly.—In 11 cases (30%), all involving old birds, females were first seen on territories other than those on which they settled. One female provided three of the cases (in different years) and two provided two cases each, perhaps suggesting that delay in pairing is associated with individual characteristics. The bird that in 3 years moved about before pairing was also the first female to arrive on the study area in four straight breeding seasons; there may have been a connection between her early arrival from migration and her failure (inability?) to select a male or breeding location immediately.

Most (seven) temporary associations with males lasted about 1 day, but one lasted 4 days and another 5 days. Two interesting cases will be described. (1) A female associated with a different male on each of 2 days, disappeared for 21 days, then returned to the study area to mate with a polygynous male that had not been an earlier associate. Probably she had paired elsewhere in the interim (see Chapter 30). (2) A female during 2 days was courted by four males, none of them her ultimate mate. An associate and I stationed ourselves 250 m apart on two territories separated by a ravine and woods. The female moved back and forth between these two territories about every 15 min, evoking courtship at each appearance and loud advertising after each disappearance. She switched between these males seven times in 105 min. Next day, she joined her mate for the season.

CHAPTER 11

THE TIMING OF PAIR FORMATION; AGES OF PAIRS; REMATINGS

PAIRS FORMED AT BEGINNING OF SEASON

Date of pair formation.—As noted in Chapter 10, short of the point at which laying began I found no objective criterion for determining with certainty that a pair had formed; but females did not leave males after laying eggs unless the nest failed. Therefore, a “pair” is a male and female whose association led to the laying of an egg; the date of pair formation is the date of their observed first meeting, and the beginning of their association is called “pairing.” The period that began when a male acquired a territory in spring and that ended the day before pairing is the “pre-pair-formation period”; the term is applicable to the individual males and not to the population as a whole. In the 10 years in which I followed the activities of at least seven males, the last male to pair did so no more than 22 days after the first male. Accordingly, pairs formed in the 22 days beginning with the year’s initial case of pairing are regarded as established at the beginning of the season; pairs formed subsequently were formed in mid-season. The period that began each year when the first pair formed and that ended on the day the last pair formed at the beginning of the season is the “population pair-formation interval.”

Time is measured in days, and part of a day is counted as a whole. The statement that a bird arrived on a territory or paired on a designated date is based on observations made at least daily. It is impossible to exclude the chance of error of 1 day; cases thought likely to involve greater error have been rejected.

A source of possible error is that unbanded birds supplied some of the data. Error could arise if an unbanded individual replaced another of its sex on a territory without my knowing it. However, continuity in behavior and individuality of appearance and voice permitted individuals to be recognized from day to day in most cases, and I believe the possibility of error is slight. Drawing data from unbanded birds is unavoidable; few females showed site fidelity, so banded females were rare at the beginning of the season. Most males relied upon were color banded.

A few polygynous bonds formed at the beginning of the season, but to avoid complication these are excluded from the results.

Pooling all years, the earliest of 154 dates of pair formation at the beginning of the season was 21 April and the latest was 15 May. The mean date was 1.5 May (SD 5.0 days).

Annual variation in date of pair formation.—Substantial annual differences existed, probably associated with variation in weather, as discussed below. During each of the 10 years (see Table 19) in which I learned the dates of pair formation of at least seven males, including the first and last male that paired, extreme dates of first pair formation were 21 and 29 April; the mean was 25 April. Extreme dates of last pair formation were 3 and 15 May; the mean was 9 May.

TABLE 19
DATES OF PAIR FORMATION¹ AND DURATION OF PAIR FORMATION INTERVAL²
IN 10 SELECTED YEARS

Year	Number of pairs	Earliest pair formation	Interval in which approximate middle two-thirds of pairs formed		Latest pair formation	Duration in days of population pair formation interval ²
			Extreme dates	Duration in days		
1953	10	29/4	1/5-5/5	5	7/5	9
1954	8	23/4	24/4-29/4	6	9/5	17
1958	22	25/4	29/4-8/5	10	11/5	17
1959	17	27/4	30/4-5/5	6	8/5	12
1960	18	24/4	27/4-5/5	9	13/5	20
1961	16	24/4	1/5-10/5	10	15/5	22
1962	15	28/4	29/4-5/5	7	13/5	16
1963	12	21/4	28/4-4/5	7	5/5	15
1964	15	22/4	23/4-1/5	9	4/5	13
1965	7	23/4	24/4-3/5	10	3/5	16

¹ The date of pair formation is that on which the members of the pair (defined on page 89) met. Only years with at least seven data are considered.

² The population pair-formation interval is the period required for all territorial males under observation to gain a mate at the beginning of the season.

The population pair-formation interval varied between 9 and 22 days (Table 19); for the 10 years the mean was 16 days. Years in which pairing began late did not tend to have a shorter interval. Table 19 shows annual dates and durations of the interval in which approximately the middle 66% of the territorial males paired. The rapidity with which this large segment of the population paired is notable; e.g. in 1959, 12 males paired in 6 days.

Effect of weather.—Fewer pairs formed on cool days than on warm, but rainfall at the levels experienced during the study appeared to have no effect on pair formation. I proceeded as follows in investigating relationships between pair formation and weather. In the eight population pair-formation intervals of 1954 and 1958–1964 were a total of 132 days (see Table 19). The weather on each calendar day was classed as warm-dry, warm-rainy, cool-dry, or cool-rainy. A day was regarded as warm if its mean temperature equalled or exceeded the long-term mean for the date (Visher 1944: 476); otherwise it was cool. Measurable precipitation marked a day as rainy. During the years in question 124 pairs formed at the beginning of the season. Table 20 presents observed frequencies of pairing on days having the four classes of weather, as well as expected frequencies under the hypothesis that weather had no effect. If the separation into precipitation subclasses is ignored and data for pooled warm days compared to data for pooled cool days, adj. Chi-square = 8.5; df = 1; $0.005 > P > 0.001$. Data for all rainy days are not different from those for all dry days, and this is also true when warm-rainy days are compared with warm-dry days and cool-rainy days compared with cool-dry days.

In addition to affecting timing of pair formation by regulating the arrival of migrants (reference to weather records for 1953 and 1961, the years with the shortest and longest pair-formation intervals, will demonstrate this; see Chapter 3), weather probably affected pair formation by altering the time budget of unpaired birds and causing them to increase the time devoted to feeding. However, I observed this only in a qualitative way.

TABLE 20
NUMBERS OF PAIRS FORMED, ACCORDING TO WEATHER ON DAY OF
FORMATION

	Weather on calendar day ¹				Totals
	Warm-dry	Warm-rainy	Cool-dry	Cool-rainy	
N, days	53	31	33	15	132 ²
N, pairs formed					
Observed	59	36	23	6	124
Expected ³	49.8	29.1	31.0	14.1	124

¹ Data are from 1954 and 1958–1964. A day was warm if the mean temperature was as high as or higher than the long-term mean for the date, as published by Visher (1944: 476). A day was dry if no measurable amount of rain was recorded.

² The aggregate number of days in the pair-formation intervals of all years was 132.

³ Expected frequencies are calculated on the null hypothesis.

Age of members of pair.—Old females paired at an earlier date than yearlings, but it is not clear whether a similar age difference existed among males. (Pertinent data on males appear on pp. 94–95.) I compared mean dates of pairing of 31 yearling females and of 87 older females, using calendar rather than relative dates because the cases in each subsample were similarly distributed among the various years. An individual is counted once for each year she supplied data. The mean date of pairing of the old females was 30.3 April (SD 4.5 days). The comparable date for the 1-year-olds was 3.4 May (SD 5.1 days); $t = 3.18$; $df = 116$; $0.005 > P > 0.001$.

As shown in Chapter 3, data on arrival of migrants indicate a difference between female age classes similar to the one just shown. No observations suggested an age difference in speed of pairing after arrival, and the 3-day difference in mean date of pairing was probably simply a function of different migration schedules.

The pre-pair-formation period.—I recorded the pre-pair-formation period of 154 males, counting an individual once for each year it provided the information. The shortest period lasted 1 day and the longest 22 days; the mean was 7.8 days (SD 4.7 days).

Male arrival date as affecting pre-pair-formation period.—Pooled data from 10 years (1953–1954 and 1958–1965, selected because in each I observed at least seven males' periods) reveal a significant negative linear regression of length of pre-pair-formation period on date of male arrival on territory. For 140 cases, $Y = 10.72 - 0.49X$. The standard error of the regression coefficient = 0.09; $t = 5.19$; $df = 138$; $P < 0.001$. For this analysis I treated arrival day in each year as day 1 and numbered all subsequent days successively. This procedure does not avoid distortion produced by the facts that the male population returned in a shorter period in some years than in others and that data for the various years are unequal in number.

Table 21 segregates the data according to year. In only four years was the value of t significant at the 5% level or beyond; but the more important point is that only one annual regression coefficient was greater than -1.0 ; one coefficient even has a positive sign. That is, in all but one of the 10 years, the average male arriving at an early date tended to obtain a mate before the average male that returned later. True, the early male had a longer pre-pair-formation period

TABLE 21
REGRESSION OF DURATION OF PRE-PAIR-FORMATION PERIOD¹ ON RELATIVE
DATE² OF ARRIVAL OF MALE, ACCORDING TO YEAR

Year	Regression equation	df	Value of <i>t</i>
1953	$Y = 5.18 - 0.21X$	8	-0.91
1954	$Y = 4.88 + 0.11X$	6	0.20
1958	$Y = 12.74 - 0.71X$	20	-3.29**
1959	$Y = 13.69 - 0.86X$	15	-5.29**
1960	$Y = 10.86 - 0.29X$	16	-1.20
1961	$Y = 12.19 - 0.22X$	14	-0.32
1962	$Y = 5.77 - 0.16X$	13	-0.98
1963	$Y = 13.16 - 0.64X$	10	-2.53*
1964	$Y = 8.56 - 0.26X$	13	-1.16*
1965	$Y = 24.18 - 1.65X$	5	-3.53

* Indicates values of *t* between the 5% and 1% level of significance. ** Indicates values at or beyond the 1% level.

¹ The pre-pair-formation period began on the day a male acquired a territory and ended with the day before he obtained a mate.

² The day on which the first male acquired a territory in each year was day 1, the following day was day 2, etc. See page 22.

(an average of 0.5 days for each day he returned before another male), but for each day he arrived earlier he averaged 0.5 days earlier in pair formation. (In 5 of the 15 years for which I have the information, the male that arrived earliest paired with the first female that settled on the study area.)

Existence of a rather precise timing mechanism controlling the individual's migration schedule was inferred from data in Chapter 4. Since early return increased chances of early pairing, any advantage that might arise from early pairing would be selected for and would enter into the balance of factors determining the timing of the male Prairie Warbler's arrival. Before discussing the possible advantage of early pairing, I shall consider two other potential consequences of early arrival.

Migration into Indiana in mid-April instead of in May would probably be disadvantageous if availability of food and adequacy of shelter were the only factors considered (see p. 26 and Fig. 5). Given the rapidity of the development of foliage and emergence of insects in May, a 10- or 15-day postponement of arrival would usually bring the migrant into a considerably more favorable environment. Counter-pressures must be considerable to cause return when the energy cost of finding food and maintaining body temperature is higher. Second, early migration into Indiana probably does not confer an advantage in acquiring a territory, although historically breeding sites may have been scarce enough to create this kind of pressure. The study area always held some vacant habitat, now in one field, now in another, whose suitability was demonstrated by its being occupied during most years. The frequency with which returning males abandoned former territories and set out to relocate (p. 31) may be some evidence that there was no land shortage, although this behavior could be advantageous even in a condition of land shortage. Further, the existence of fairly stereotyped behavior by which 2-year-old and older males easily reclaimed former territories from usurpers (Chapter 6) suggests that neither now nor since the evolution of the behavior has early arrival been essential to the old male's gaining of a territory. As for females, they probably are not under great pressure to return early

in order to find mates and breeding locations—the sex ratio is equal (see Chapter 31) and polygyny is available to females—although the early-arriving female presumably has a wider range of males and/or territories to select from.

In sum, early return seems to confer no great advantage in terms of resource acquisition. However, a great advantage would accrue to the early-returning, early-pairing male under the following conditions, all of which were satisfied on the study area: (1) if early pair formation increased chances of early nesting (see pp. 111–112); (2) if, even though a large proportion of nests failed to produce fledglings, females renested persistently and as a result ultimately often brought off young (see Chapter 33); and (3) if timing of the end of the female's ability to renest was independent of the number of her previous nest attempts (see p. 427; compare pp. 170–172). Under these conditions, early return would tend to increase the period in which a male had a mate, therefore the number of nests she would have an opportunity to build, and in turn the probability that the male would leave offspring. In addition to this higher probability of producing first-brood young, an early start on nesting increases chances of having a second brood. Whether a female attempted a second brood was closely related to the date the first brood left the nest (Chapter 34); and since second-brood attempts had the benefit of the higher late-season success rates (Chapter 33), the added advantage of an early start on the first-brood effort seems clear (see also p. 398).

Data (p. 188) reveal that the interval between pairing and the female's laying of egg 1 regressed negatively on the date of pair formation, but the regression coefficient was only -0.15 days. Combined, this coefficient and the coefficient of regression of the pre-pair-formation period on date of arrival indicate that on the average the beginning of egg laying by a male's mate was advanced about 1.4 days for each day his arrival on his territory was accelerated (within normal, observed limits of arrival dates). Since the mean date of laying of egg 1 in first nests was about 14 May (p. 184) and the date when about 50% of all females ceased to be able to replace nests was about 25 June (p. 423), the period in which the average female laid eggs was only about 45 days long. Therefore, for each day a male returned early to the study area he tended to increase by about 3% the length of the period during which he had opportunity to have a mate in reproductive condition.

Differences in pre-pair-formation period, according to year and section of study area.—Table 22 distributes the 154 pre-pair-formation periods among the years of the study, giving mean and extreme length for each year and the standard deviation for years in which there were at least 7 cases. The annual variation, from a low mean of 4.2 days in 1953 to a high of 11.4 days in 1961, is probably attributable largely to weather differences affecting time of arrival of females. Length of the annual mean pre-pair-formation period and length of the population pair-formation interval were positively correlated (compare Tables 19 and 22); $r = 0.62$; $df = 8$; $P \approx 0.05$.

Some annual variation may have been associated with differences between the two sections of the study area, the University Farm and the Griffey Tract (see Introduction). Mean duration of 32 pre-pair-formation periods on the University Farm is 6.2 days (SD 4.2 days) and for 122 periods on Griffey 8.1 days (SD 5.0 days); $t = 1.97$, $df = 152$; $P \approx 0.05$. In a test of the slope of the

TABLE 22
DURATION IN DAYS OF PRE-PAIR-FORMATION PERIODS,¹ 1952–1966

Year	Males, N	Pre-pair-formation period		
		Mean	Extremes	SD
1952	4	8.3	3 – 13	—
1953	10	4.2	2 – 7	1.8
1954	8	5.4	1 – 14	4.0
1956	3	4.3	1 – 10	—
1957	3	5.0	2 – 8	—
1958	22	7.8	1 – 19	5.2
1959	17	7.6	1 – 16	4.2
1960	18	9.0	3 – 18	4.2
1961	16	11.4	1 – 22	5.4
1962	15	4.6	1 – 9	2.6
1963	12	9.4	2 – 17	5.0
1964	15	7.3	3 – 14	3.2
1965	7	9.6	1 – 22	7.8
1966	4	5.5	2 – 7	—

¹ The pre-pair-formation period began on the day a male acquired a territory and ended with the day before he paired. See page 89 for the definition of pair. Only pairs formed at the beginning of the season (page 89) are included.

regression of duration of pre-pair-formation period on relative arrival date of the 32 University Farm cases ($Y = 6.92 - 0.18X$), $t = 0.69$ and there is no evidence that a regression existed. In contrast, the equation for the 122 Griffey Tract cases is $Y = 11.40 - 0.52X$; $t = 5.56$; $df = 120$; $P < 0.001$. By analysis of covariance I tested (not shown) the homogeneity of the two regression coefficients. $F = 6.59$; $df = 2$ and 150 ; $P < 0.01$, and I conclude that the regression existed only in the data from Griffey. Because I never studied the two tracts in the same year, much or all of the apparent difference between them probably is attributable to annual weather variation. Data from Griffey differed from year to year, so it is unnecessary to resort to explanations involving difference in location. Nevertheless, important vegetational dissimilarities on the two tracts (Introduction and Chapter 29) clearly did cause differences in certain behavior (e.g. nest placement; see Chapter 15), and it is possible that tract differences had some effect on pre-pair-formation periods.

Age of male and pre-pair-formation period.—I compared relative arrival dates (see p. 22) and pre-pair-formation periods of 56 banded old males with comparable data for 31 males either known or thought to be yearlings (see p. 22) and obtained conflicting results. To reduce effects associated with annual variation and possibly with tracts, comparison was restricted to cases from the Griffey Tract. Importantly for the discussion below, the proportions of birds in the two age classes were not identical from year to year, which may have biased the data. Mean relative arrival dates of the two groups differed significantly: that of old males was day 4.7 (SD 3.3 days), that of yearling males day 7.6 (SD 4.0 days); $t = 3.64$; $df = 85$; $P < 0.001$. Mean length of the pre-pair-formation periods also differed; for old males it was 9.4 days (SD 4.9 days), for yearlings 7.8 days (SD 4.6 days). Analysis of covariance reveals that the regression coefficients and adjusted means for the two subsamples were homogeneous ($F = 0.30$ and 0.15 , respectively). Accordingly, there is no reason to believe that being a yearling

exerted any independent effect on length of a male's pre-pair-formation period; the simple interpretation is that a yearling's period was shorter if his arrival date was later, as it usually was.

A different result is obtained when pre-pair-formation periods of 19 old and 19 young males are matched as pairs in an effort to eliminate bias arising out of annual differences. Members of each pair are alike in that (1) their arrival dates fell within a 3-day or lesser period in the same year, (2) their territories were either both marginally or both centrally located relative to the clusters of territories in fields, and (3) their territories were about the same size. The mean length of the period for yearlings is 10.1 days, of older males 7.0 days; the standard deviation of differences is 6.2; $t = 2.33$; $df = 18$; $P < 0.05$. Only four old males in the 19 matched pairs had longer pre-pair-formation periods than their younger counterparts; there were two ties. Applying the sign test where $N = 17$ and $x = 4$, $P = 0.025$.

In sum, the adjusted mean pre-pair-formation period of yearlings was not shorter than that of old males, and tests eliminating annual differences and perhaps differences among territories suggest that it may have been significantly longer. If this last is true, the behavior of old males may be more effective than that of yearlings in attracting females (compare p. 364).

Ficken and Ficken (1967b) summarize data indicating that in the American Redstart first-year males are less successful than old males in acquiring mates. Redstarts are atypical parulids, however, in that there is conspicuous delayed maturation of plumage characters in the male, accompanied by age-specific differences in reproductive behavior and success.

Although perhaps not likely, an individual's pre-pair-formation periods might tend to lengthen or shorten with increasing age. I therefore matched and compared two pre-pair-formation periods of each of 18 banded males that bred on the area at least three seasons. Only the periods from the second and third years spent on the same territory were analyzed, and the test was limited to birds that were consistent in their two relative arrival dates (Chapter 4). Data were drawn from 10 different seasons, and effects of annual weather differences probably averaged out. No differences associated with ageing were suggested.

Characteristics of territory and length of pre-pair-formation period.—I recorded characteristics of many territories, as detailed in Chapter 29, but found no association between length of pre-pair-formation period and shape of territory, number of surrounding territories, or various vegetational parameters. Probably the study area was too homogeneous to reflect female preferences in these respects, or my measurements were too crude.

Interestingly, four males with isolated territories, probably beyond earshot of other males, all obtained mates after normal periods.

Chapter 31 reports relationships among a male's territory size, pre-pair-formation period, and success in becoming polygynous. I therefore expected a negative correlation between territory size and duration of pre-pair-formation period among all males, both polygynous and monogamous. To test the hypothesis, I selected the 48 Griffey males whose territory sizes, relative arrival dates, and pre-pair-formation periods I knew, and performed a multiple regression analysis. Contrary to expectation, there was no negative regression of pre-pair-

formation period on territory size independent of relative arrival date. It appears therefore that in this sample territory size did not affect the promptness with which males obtained mates, a result that is difficult to reconcile with the larger territories, shorter pre-pair-formation periods, and other reproductive advantages of polygynous males (see Chapter 31).

PAIRS FORMED IN MIDSEASON

Dates of pair formation.—Pair formation continued throughout the breeding season, both because polygynous relationships were established and because many bonds dissolved, one or both members left or died, and other Prairie Warblers appeared and paired. The latest instances of pairing occurred on 10 July, at the very end of the nesting season.

Previous histories of individuals that entered late-formed pairs and the movements of these birds are dealt with in Chapters 30 and 31. Frequencies of appearances and disappearances of males and females and the sexual relationships that they formed are analyzed in Chapter 31.

Dates of pair formation following midseason acquisition of territory by male.—On page 344 are reported six instances in which males took over land evacuated by other males and four instances in which males took possession of land that had not been occupied previously that season. Extreme dates of the formation of pairs following these 10 instances were 21 May and 10 July; the mean date was 12 June (SD 16 days).

Dates of pair formation following arrival of female on male's original territory.—The pairing of 36 females on the study area in midseason is reported on page 346; these birds joined males holding territories they had occupied since the beginning of the season. Extreme dates in these cases were 18 May and 10 July; the mean was 14 June (SD 15 days). Five pairs formed in July, when little of the season remained (see Chapter 34). This remarkable fact emphasizes both the speed with which pairing could occur and the persistence of the effort to reproduce (see Chapter 33).

The midseason pre-pair-formation period.—The midseason pre-pair-formation period is the number of days required for a male newly arrived on a territory in midseason to acquire a mate there or for a male on a territory long owned by him to obtain a replacement for a mate that had disappeared. The period began on the day the male arrived on the territory in midseason or lost his earlier mate on his original territory; it ended with the day before the female was acquired. The concept of pre-pair-formation period is inapplicable to polygynous pairing with a second female. The definition of the period also excludes five cases of males that took over territories and paired with the mates of the former owners of these; but certain details of such cases will be reported.

The duration of 23 pre-pair-formation periods is known, 19 between disappearance of the mate of a monogamous male and her replacement and 4 between a male's midseason establishment of territory and acquisition of a mate. The extremes were 1 and 25 days; the mean was 8.2 days (SD 6.4 days).

Table 23 distributes the 23 periods according to approximate half-month intervals in which the pairs formed. Variation according to date is not clearly

TABLE 23
PRE-PAIR-FORMATION PERIODS OF UNMATED MALES THAT ACQUIRED FEMALES
IN MIDSEASON,¹ ACCORDING TO DATE OF PAIR FORMATION

	12-31 May	1-15 June	16-30 June	1-10 July
N	4	5	11	3
Mean, days	2	9	7	5
Extremes, days	1-4	4-13	2-14	2-10

¹ Pre-pair-formation period and midseason are defined on pages 96 and 89, respectively.

shown, but periods in May may have been shorter; it may have been easier to attract a female then, when a few late-migrant females were still arriving.

As indicated, four males took over ownerless territories on which were incubating females; these latter continued to incubate. The time that elapsed between departure of the original male and arrival of the replacement was 10, 6, and 6 days in the cases for which I have the information. In a fifth and different kind of case, a latecomer evicted a male from half of a large territory; the ousted bird had two mates, one of which was incubating on the land the owner yielded; she continued to incubate. In this case, of course, no time elapsed between replacement of males.

In four of these five cases of change in territory ownership the females already on the site, when ready to breed again, paired with the new owners. Two males had been on the territories 1 and 3 days, respectively, when the females' current nests failed. One female brought off the brood fathered by her departed mate and did not begin a second-brood nest, for which the replacement male was her mate, until 35 days after the latter acquired the territory. In the fourth instance I lack sufficient information; and in the fifth case the female was not responsive to the courtship of the replacement male and left the territory when her nest failed.

AGES OF MEMBERS OF PAIRS

Pairs formed at beginning of season.—To learn whether either yearling or older females showed a preference at the beginning of the season for yearling or older males I used data from 80 pairs for which I knew or inferred (see p. 22) the ages of both members. An individual was counted once for each year in which it supplied information.

There was no tendency for an age class of either sex to pair preferentially with

TABLE 24
AGES¹ OF MEMBERS OF 80 PAIRS FORMED AT BEGINNING OF SEASON²

Males	Females		Totals
	1 year	Older	
1 year	7	18	25
Older	11	44	55
Totals	18	62	80

¹ Males were aged as described on page 22. Females were aged by plumage characters or by knowledge of the dates on which they had been banded.

² See definition, page 89.

TABLE 25
 DATES OF MIDSEASON PAIR FORMATION¹ INVOLVING FEMALES OF KNOWN
 AGE,² ACCORDING TO AGE OF FEMALE

Age of female	Date			
	18-31 May	1-15 June	16-30 June	1-10 July
1 year	4	6	4	0
Older	5	3	8	4
Total	9	9	12	4

¹ Pair and midseason are defined on page 89.

² Females are classed as 1 year old or older; aging was by plumage characters or was based on knowledge of the dates on which they had been banded.

an age class of the other (Table 24; $0.75 > P > 0.50$). It may be asked why, since old birds of both sexes arrived earlier than young birds (Chapter 3), the data do not show a tendency for old females to pair with old males. Several reasons are suggested: (1) The migration schedules of the age classes may not have differed enough to produce the suggested result in a sample of only 80 pairs. (2) Relocation by some old males (Chapter 5) delayed their pairing and tended to counteract the effect of their earlier arrival. (3) Some females, including old ones, did not pair immediately upon arrival (p. 88), thereby increasing opportunities of young females to find and pair with unmated old males.

Pairs formed in midseason.—Twenty-nine males that I aged gained new mates in midseason; 18 males (62%) were older than 1 year old and 11 (38%) were yearlings. The ratio of old birds to yearlings in the population was 2:1 (Chapter 38), and neither male age class showed a special tendency to be unmated in midseason; therefore it appears that in midseason females paired with equal readiness with males of either age. The mean number of days required to gain new mates was 7.0 in the case of eight old males for which the point is known, 5.5 for six yearlings. Further, 5 males of known or inferred age lost mates and advertised with no success; 3 were old and 2 were yearlings.

The ages, when known, of female members of pairs formed in midseason are shown in Table 25. Two interesting points are suggested: First, the number of yearling females that paired between 1 June and 15 June was 6 and of old females, 3. Since the ratio of yearlings to old birds among all breeding females was 1:2, the 6:3 ratio of midseason pairings by yearlings may suggest that they were more likely than older females to leave first mates and pair again. Second, from 15 June on, 12 old females paired on the study area, whereas only 4 yearlings did so. To consider the extremely late cases of pair formation, those in July, the four females of known age that joined males in July were old. The latest pairing by a yearling female was on 20 June; 10 old females paired after that. Since the first point indicates, at the least, that yearlings formed replacement pairs readily, the second suggests that they quit doing so at an earlier date than old females. Chapter 41 points out that yearlings began postnuptial molt before old birds.

REMATINGS OF PAIRS SURVIVING FROM EARLIER YEARS

On 13 occasions a banded female returned to the study area when her banded mate from the previous year was holding all or part of the territory on which she

had formerly nested. There were six rematings (compare Brackbill 1959). In five of these the female paired at the beginning of the season with the mate of the preceding year; two cases were provided by the same female, i.e. she and the male were mates for 3 successive years. In the sixth instance, the female was courted by her former mate but paired with his neighbor; however, immediately after bringing off her first brood she moved across the territory line and in July raised a second brood with the former mate. The behavior of birds that paired with each other for a second or third season showed no unusual features.

The seven cases of failure to remate may be subdivided into two groups: females that reoccupied former sites, and females that moved. Three females paired with males whose territories overlapped the territories of these females' mates of the year before; thus these females reoccupied the old breeding site. One of them, however, had two former mates on hand, so that she did reject one former breeding site, the one occupied at the more remote date. This was the only female of the three that was courted by the former mate; when the other two females arrived, their former males were already paired and were occupied with courtship.

Four females that did not join former mates are known or presumed to have moved to new locations. Only one location was found; the other females left the study area (they were seen later, hence had not died). The former mates of all four females in this group were already paired when the females returned.

As Hann (1937: 152-154, 209) and Mayfield (1960: 54) suggest with regard to other parulids, the evidence is that rematings were produced indirectly by the site attachment of former mates, which caused them to meet again, not by attachment to each other. It is especially interesting that when the former breeding site had been divided between an earlier mate and a strange male, one female showed no preference for her earlier mate even though he courted her. (The importance of the site rather than the male is suggested by the fact that one female occupied the same site and built her nest in a very small area for 3 successive years, mating with a different mate each year. However, her former mates had not returned.)

CHAPTER 12

BEHAVIOR DURING PRE-NEST-BUILDING PERIODS

Behavior of the pair was much the same before the building of all nests, and the information below applies equally to periods before first nests of the season, replacement nests, and second-brood nests, except as specifically noted.

The pre-nest-building period of the first nest began when the courtship behavior described in Chapter 10 became infrequent, and it ended at nightfall on the day before the female started to build. The replacement period, i.e. the pre-nest-building period of replacement nests, began on the day of nest failure and ended at nightfall on the day before start of building. The pre-nest-building period of the second-brood nest began the day the fledglings left the first-brood nest and ended at the close of day before commencement of the second-brood nest. A distinction is drawn between nests and fragments. Fragments are structures left incomplete because the female apparently was insufficiently motivated to build, rather than because of interference by predators, weather, etc.

Some behavior is described in this chapter because it first appeared regularly just before building began, even though it continued into subsequent stages of breeding.

TRANSITION INTO PRE-NEST-BUILDING BEHAVIOR

The transition to pre-nest-building behavior of first nests was simple progression from the next earlier stages; but with replacement and second-brood nests the opposite, a reversion from a more advanced stage, occurred. This section deals largely with the latter kind of transition and the speed with which Prairie Warblers could terminate parental behavior and revert to prebuilding behavior.

Transition before first nests.—As the displays characterizing pair formation became infrequent, the male introduced new song versions and sang less loudly and less often (see Chapter 8). The female quit crossing territorial boundaries; fighting diminished. The pair foraged near each other for long periods, with only occasional watchfulness and tenseness apparent between them. When they were separated the male sang more frequently. Soon the female began to explore for nest sites.

Transition before replacement nests.—Nests lost during building: Nest failures during building were almost always followed by immediate resumption of pre-nest-building behavior; no transitional activity was observed. For example, twice Blue Jays visited nests under construction and caused the females immediately to desert. Both began nests within a few hours on the same day.

Nests lost during laying: After nest failure during laying the female probably almost invariably had an already ovulated egg in the oviduct. If the failed nest was intact, she sometimes (seven cases) laid this and even additional eggs in that nest, then abandoned the nest; three females laid the full clutch before abandoning. I interpret these cases as dumping of eggs, since the females did not incubate.

Dumped eggs were never found on the ground, but twice I caught females with eggs ready to be laid and visible under the skin; when released, the birds did not go back to their nests and must have laid the eggs elsewhere. One damaged nest was used for dumping; egg 1 was laid on top of it after it had been crushed flat, and next day another fresh egg lay broken on the ground below it. In all cases of laying after nest failure, females were never observed to revert to pre-nest-building or to building until they had finished egg laying.

Various reactions to experiments in which I removed eggs from nests are related to these episodes, as are cases in which females laid eggs in, then abandoned, nests that had been parasitized by cowbirds (see pp. 174–175).

Nests lost during incubation: Females probably witnessed many cases of nest predation during incubation; if so, fright may have affected the speed with which they were able to revert to pre-nest-building behavior. When eggs were taken without the female's witnessing the loss, abandonment of the nest was gradual, as the following and other experiments showed: At 1110, I took all eggs from a replacement nest of a female that had been incubating 7 days. She returned at 1127, sat in the nest until 1142, then left. At 1157, she went to the nest and called Chek eight times as she sat in it (incubating females normally are silent). She stayed only 2 min, turning and rising frequently, then left but returned and incubated from 1206 to 1223 and 1241 to 1257. At 1340 she approached the nest and called Chek but left; at 1347 she perched in the nest tree 5 sec. At 1348, she went to the nest and looked in for 10 sec, then abandoned it permanently. At 0800 the following morning she was exploring for a nest site; the male made a sexual chase, and she responded with flight-to-male. She began to build about 1100. (Several times I inspected nests that had held eggs on the day before and found females sitting in the empty cavity.)

Nests lost during nestling interval: An example of transitional behavior after loss of nestlings is the following: A nest containing three young 8 days old was emptied by a predator shortly before 1115, when I arrived; the nest held a wet fecal sac. At 1120 the male carried a caterpillar to the cavity four times, then ate it. At 1125 the female went to the nest and removed the fecal sac. She began to forage nearby while the male followed her closely. Within 10 m of the nest, the female suddenly began to solicit copulation (see below) but turned on the male and drove him away as he started to mount. She then went to the nest, hopped around it, looked in for 1 min, preened, and left the vicinity. At 1150 and 1200 she again approached, at 1204 caught an insect and three times carried it to the rim. Next morning she began a replacement nest. (Carrying of food to, and fecal sacs from, nests from which young had just flown was seen several times. A male once proffered food to the space from which I had removed a newly-failed nest and eggs 24 hours earlier.)

Twice males probably briefly tended nestlings that hatched in nests already deserted by females. Both males also exhibited normal attentiveness to the females as these searched for new nest sites and began to build. An example: A female abandoned a nest and the one egg remaining after a predator had taken three young that had just hatched. Next morning the pair was searching for a nest site; the egg hatched about 1200. One hour later the shells were gone from the nest,

and the male was near it; the female had begun to build. Next day the young was dead; but it appeared to have food in its digestive tract.

Transition before second-brood nests.—When first-brood fledglings were present, both adults alternated pre-nest-building and parental behavior. Females appeared more attentive to young than did males. Some females engaged in bouts of exclusively parental behavior and bouts of prebuilding behavior in which the young were completely ignored, but one intermingled the two activities in rapid succession. (As described on p. 144, females also interrupted nest building to care for fledglings.) In males, interest in the female seemed paramount most of the time, and butterfly and moth flights were frequent.

What caused the male, which often accompanied the female at all stages of the cycle, to treat her in one fashion during the incubation period or nestling interval but differently if the nest had just failed? The stimulus was almost certainly the female's behavior. She ceased the rapid foraging typical of the incubation and nestling stages (see p. 491) and was available for continuous association, since she no longer sat on the nest. The male followed her much of the time; she then began to explore for a nest site, which stimulated the male behavior characteristic of that stage. In addition to a few direct observations of the sequence described, evidence that the female's behavior determined that of the male follows: Males accompanied females quietly and usually unexcitedly and without courtship for long intervals during egg laying, i.e. when the females engaged in no pre-nest-building behavior. Twice after females were injured in netting accidents males regularly accompanied and foraged quietly near them with no sign of the behavior characteristic of the prebuilding period, to be described.

SEARCHING FOR AND SELECTING NEST SITES

Except as suggested below, the female appeared to select the nest site. Usually she did not first focus on a part of the territory and then select a site within it, but one female largely confined herself to a very small area for 2 days and then picked a nest tree in that area. Other situations in which there was reason to believe that the precise location was selected after preliminary choice of a restricted area were a few cases in which females built fragment(s) in a single tree, then built a nest in it.

Early in the season, searching for a site usually began several days after pairing, but a few females began on the day they joined males. Females that paired in midseason often started to search within 2–4 hours of pairing. Similarly, the period of searching often lasted 3–4 days early in the season but only 1–2 hours when pairs formed in midseason (see Chapter 11).

Behavior of female.—Searching took place at all times of day, the female going from tree to tree, at times quickly and at others very slowly; sometimes she visited only one or two forks and resumed foraging. Her course was erratic, probably upward through a tree or shrub more often than downward; having moved into the upper section of a tree she then frequently flew to a low point in another. Half the time progress was silent; some birds called Chek and/or Seep occasionally.

Behavior while in a fork included one or more of the following, which appear to represent steps on a scale of increasing motivation: perching quietly, squatting,

pivoting, interrupting pivoting to push one foot or both feet alternately outward or downward, thrusting one or both wings outward and upward. Extension of the limbs may have provided the bird with information about the site's suitability. All behavior just mentioned continued as early-stage building activities (see Chapter 16). The duration of the average series of acts in one site was 30–60 sec (maximum 4 min).

Periods of exploratory movement through trees were irregular in length. Brief, isolated acts of squatting apparently were at times triggered by chance contact between the foraging female's belly and a branch. At the other extreme, just before beginning to build females often spent most of the time, for 15–20 min intervals, behaving as described.

Behavior of male.—The male usually followed and watched the female at about 5 m distance; sometimes he flew right over her and landed 1–2 m beyond. Many flights were display flights; e.g. the male would glide down to a fork in which the female was shaping, hover 1 sec, then perform butterfly flight away from her. Song was rare, irregular, most often at half volume or less; males occasionally sang in flight.

In some 10% of about 300 observations a male was nearly as active as his mate in visiting nest sites. Such males moved from fork to fork and sometimes executed elaborate wing, leg, and body movements for more than 1 min. In this nest shaping, the behavior of the male appeared not quite identical with movements of the female; it looked less like the preliminary trying of the site than like actual building behaviors used by females in shaping well developed nests (described in Chapter 16). Thus, in the most elaborate nest shaping, the male squatted in the site, vigorously depressed the sternal region and elevated the tail while kicking backward with the feet, and rotated the body while extending and drooping the wings, especially the wrists. (Bill movements were not seen at these times, but an unmated male once gathered spider webs, carried them to a fork, spread them around in behavior typical of a female attaching webs, then went through shaping motions for 40 sec during which he sang a loud group-A song. Some relationship between this behavior and sexual frustration seems possible; compare Morris' (1955) "factor C" in the causation of pseudofemale behavior. Also relevant are episodes, p. 144, in which males entered nests under construction and engaged in shaping movements, at times using the bill to work nest materials.)

Sometimes when a male explored he appeared to be selecting the site very carefully, repeatedly getting in and out of the fork and looking at it. Contrary to the usual sequence, one male engaged in nest shaping on the day he acquired a mate, before she had performed any observed behavior preliminary to nest building. The female often flew to watch the male, sometimes entering the fork with him and at others waiting until he got out before getting in; a few times females seemed to drive the male out, as though impatient to get in. In a variation, a female entered a site and the male then joined her in it. In these cases females occasionally had nest material in the bill. At times Twitter or Seep was called by one or both birds when close together. One male sang a full song as the female approached him.

Discussion of male behavior.—Probably nest shaping expressed intense stimulation not experienced by all males (compare the differences in the effect on males

of the female's building activities, p. 146). If it is assumed tentatively that the male's nest shaping was a display, the question of its function arises. It is most probable that shaping stimulated the female and contributed to synchronizing the sexual conditions of the pair. A display would not seem useful in acquainting the female with suitable sites, which appeared almost innumerable. Nor is any advantage apparent in the male's participating in nest-site selection. Nevertheless, in a few cases the location of the male's nest shaping was the site ultimately used, as in this example: After a male had nest-shaped 40 sec the female entered, probably for the first time, and sat 1 min while male remained nearby. She left for a moment; he went back to the spot, to be rejoined briefly by her; 3 min later she came back with the first material for the nest, which she then worked on steadily and completed. Close inspection of two other sites in which males displayed and to which females then carried material disclosed too much material present to have been brought in the load I had observed; these males had been shaping in forks in which the females had already done some building. Most male nest shaping was in forks in which no material was subsequently placed; many nests were built in locations that I never saw males enter. It is therefore probable that shaping stimulated the female and contributed to synchronizing the sexual conditions of the pair.

Ficken (1964) has described site-selection behavior in the American Redstart very like the foregoing.

MANIPULATION OF NEST MATERIAL WITHOUT BUILDING

Even at the beginning of the season occasional females pulled at or picked up and dropped nest material on the day they joined a male, but this behavior usually appeared at least 2-3 days after pairing. Most females probably first began to search for sites, and toying with material apparently reflected a state more advanced toward readiness to build. As further evidence, after a few nest failures late in the season females that did not rebuild explored for nest sites but did not pick up nest material.

Birds that joined males and formed pairs in midseason often selected a site, bypassed the stage of manipulating material, and began immediately to build. Similarly, females that built replacement nests usually engaged in no toying with material, but a few did so as much as at the beginning of the season.

Ordinarily the substances gathered were bast fibers or plant down rather than the spider and insect webs that were usually the first items carried to true nests. Thus the birds picked up material appropriate only for later stages of true building (see Chapter 15). Behavior ranged from casual tugging to persistent pulling of bast fibers in the manner described on page 141. The material was sometimes dropped immediately, sometimes held briefly, sometimes carried aimlessly for a few seconds. Placing it on the first perch on which the female landed probably reflected a more advanced state; and carrying it directly and with apparent purpose to place it in a tree, to which, however, the female never returned, was still more advanced. Birds that placed material in suitable tree forks did not always do so in the manner of females starting to build true nests: instead of carrying the fibers into the site and then putting them in place, the females

inserted them while perched outside the site. This method of insertion is used only after true nests have reached a late state of construction (p. 140). Therefore there is a parallel between the form of insertion behavior and the fact that the materials were often of a type used late in building.

BUILDING OF FRAGMENTS

Many birds built one or more fragments before building a complete nest, especially the initial nest of the season. Several cases of such abortive building also occurred late in the season and involved females apparently no longer able to reproduce. Fragmentary nests varied from a few strands to well-made structures lacking only a lining. The following discussion considers only those on which builders worked some 2 hr or more. Elimination of lesser fragments is arbitrary, except that probably all females carried a few strands of material at the beginning of the season.

Appearance; location.—All but about 10 of approximately 125 fragments that I found looked indistinguishable from true nests on which a corresponding amount of work had been done. The exceptions were large, loose, shapeless masses. Similar shapeless masses were sometimes built under true nests (see Chapter 15); these may have been fragments on which nests were then constructed. If this is true, a probably related phenomenon (seven cases) was building a fragment, then a complete nest a few cm away in the same tree. Sites of fragments did not differ from those of nests, and female behavior in building was the same.

Number of fragments and ages of builders.—Of 188 females nesting on territories that I inspected carefully for nesting activity, 70 (37%) built 103 fragments. A female is counted once for each year she bred on the area. The same 188 females built and laid in 446 nests. Within the group of 70 that built fragments, 44 individuals built 1 each, 22 built 2 each, 2 built 3 each, and 2 built 4 each, all multiple cases occurring in single seasons. Focusing on the birds that built at least 2 fragments, only 26 females (14%) built 58 of the fragments, or 56% of the total number found.

Of the builders, 43 were aged; 15 were yearlings and 28 older females. Since this ratio (37:63%) is almost exactly that of all breeding females, building of fragments evidently was not associated with age. Mean number of fragments built by yearlings was 1.4, as against 1.2 built by older females, again suggesting no link with age.

Subsequent activity of builders.—In 97 instances I knew what females did after quitting work on fragments: 8 deserted their mates, 65 built the first nest of the season, 17 built the first replacement nest, 6 built a later replacement nest, and 1 built a second-brood nest. Estimated numbers of hours spent building fragments were 2–3 in 17 cases, 3–9 in 27 cases, 10–15 in 30 cases, and 15–25 in 23 cases. No relationship was evident between kind of activity following abandonment of the fragment and amount of work preceding abandonment.

The large number (67%) of fragments built during the pre-nest-building period of the first nest is striking, since the number of replacement nests built greatly

exceeded that of first nests because of the frequency of nest predation (see Chapter 33).

In several cases females abandoned fragments and later resumed construction of them, either to complete as nests (six cases) or again to leave them unfinished (six cases). Periods of interruption ranged from 2 to 10 days. Six birds engaged in no building in the interim; six built other fragments or nests. Two of these abandoned fragments, then built and laid in and began to incubate nests that subsequently failed to predators. They then went back to the fragments and one completed and laid in hers.

Three females built two structures simultaneously, carrying material for a while to one and then to the other. Two finally abandoned both; the other brought both almost to completion, then finished one and laid in it.

Probable causes of abandoning fragments.—If cases were correctly selected to eliminate abandonment resulting from disturbances, fragments must have resulted from motivational deficiencies of females. This presumably is why most cases fell either at the beginning of the season or the end. An indication that the behavior was attributable largely to internal state is the fact that 26 individuals failed to finish at least two nests; further, most birds that built two or more fragments built them in succession. I observed no unusual behavior in mates of females that built fragments. Histories of banded males in successive years showed no tendency for particular males' females to leave nests incomplete. Weather on days on which work ceased on 79 fragments suggests no association between abandonment and weather.

COPULATION AND RELATED SEXUAL BEHAVIOR

Attempted mounting by male.—In eight cases a male attempted to land on a female's back from a perch beside her or after a short flight toward her. One male held his bill open. One sang a group-A song while hovering over the female; the others were silent. Some females had postured as though ready for copulation while the others had not. All but one female turned and lunged at the male and drove him away. In the exceptional case, the male flew almost to the female's back; she began to quiver her wings as in soliciting (see below), then suddenly executed a side-stretch (p. 497); the male flew on without landing and she stretched several times. Heights of attempts were 1–10 m (mean 5 m); dates were 28 April–13 July. Six attempts occurred during the pre-nest-building period of the first or a replacement nest (Table 26). Four copulations were seen in pre-nest-building periods; therefore 60% of observed male efforts to mount at this stage were repelled. Efforts at later stages were more successful; see Table 26.

Ineffectual soliciting by female.—The solicitation posture of the female was the same as the position in actual copulation: legs and feet were flexed slightly; the body squatted, leaning forward, the region of the vent elevated and the back arched; the ventral feathers were fluffed, especially posteriorly, making the body seem very close to the perch and adding to the squatting appearance. The caudal region vibrated up and down slightly (seen twice); the tail was cocked stiffly upward at a 30–70° angle (compare Andrew 1961: 347) and spread, sometimes

TABLE 26
DISTRIBUTION OF COPULATIONS AND INEFFECTIVE SEXUAL ADVANCES,
ACCORDING TO STAGE OF THE REPRODUCTIVE CYCLE

Stage	Behavior		
	Copulation	Male attempted mounting	Female solicitation
Before building			
First nest	2	2	2 ³
Replacement nest	2	3	2
Second-brood nest	0	1	1
During building			
Active phase ¹	3	1	4
Inactive phase ¹	0	0	1 ⁴
Incubation period ¹	2 ³	1	1
Nestling interval ¹	0	0	4 ⁵
Totals	9	8	15

¹ The phases of building are defined on page 149, the incubation period on page 235, and the nestling interval on pages 244 and 302.

² A case of two acts of copulation within 4 min is tabulated as 1. In another case the female was incubating a second brood, the male caring for young of the first brood.

³ This includes a case of female solicitation of a male not her mate.

⁴ A second male attacked the male as he mounted, possibly preventing successful copulation.

⁵ One female was unmated, and no male was seen near her.

barely perceptibly and sometimes so much that the tips of the rectrices were distinctly separated. The neck was retracted, the bill pointed upward 35–55°; one female opened her bill 3–4 sec. Almost invariably the wings were slightly extended, the wrists depressed a little, the primaries elevated distally and quivered. The position and motion of the wings were about those of begging young Prairie Warblers (see Marler 1956: 117).

Some females adopted a barely noticeable posture at first and gradually exaggerated it as the male approached. In these cases the initial movement was lowering the anal region, and the final movement probably was quivering the wings. Other females passed immediately into full solicitation; the male usually was 1–2 m distant but occasionally was 10–15 m.

Soliciting lasted 1–60 sec (mean 8–10 sec). The apparent reaction of males when solicitation was not effective was usually indifference. (All but one case of copulation was preceded by solicitation.) However, occasionally males approached soliciting females tentatively, then turned away. Once a female followed a male for 1 m but not in the copulatory position. Another female, disregarded by a male, hopped 2–3 m to him, perched beside him, one or both of them Twittering. Three females called Chek before soliciting. In one case a male was in the act of mounting his mate when another male suddenly attacked; sexual behavior was interrupted and the attacker was repelled.

Heights at which females displayed were 0.3–7 m (mean 2.5 m in 13 cases). One solicited while carrying material during nest building, another while carrying food to a nest. Cases were rather widely distributed over the season (1 May–23 July) and stages of reproduction (Table 26). The female that invited copulation on 1 May had joined the male that day, possibly just having arrived from migration.

The stimulus for soliciting usually (nine cases) seemed to be sight of the male, with probably two exceptions: A female, evidently unmated and passing through the area, postured in response to the song, or the sight and song, of a male; he sang several times 2 m from her and after each song she solicited 1–2 sec. Another female, deserted by her mate and caring for nestlings, adopted the solicitation position when no male was visible to me; in the nest tree she held the pose steadily for 1 min, then hopped several cm at a time while constantly shifting into and out of the position for 1 min. Ficken (1963) observed American Redstarts soliciting although no males were nearby.

Three solicitations occurred during the nestling interval, the female evidently stimulated by the male's proximity as he approached carrying food. The male, showing no visible reaction, fed the young. Possibly these instances were not primarily sexual; they may have been related to cases in which brooding females quivered their wings as mates approached with food for the young (see p. 278). In other species quivering is associated with infantile behavior performed by females during courtship feeding (see Hinde 1964b: 160).

Preliminaries to copulation.—In nine observations of apparently successful copulation, the male either hopped on the female's back from immediately beside or behind her or flew (once in butterfly flight) to her back from 10 m distance or less. The female had first solicited (maximum 30 sec) in all but one case. In the latter, the pair had been foraging, the male singing faintly and the female sitting motionlessly at times; without preamble the male flew slowly to the female, which assumed the proper position when he reached her.

Behavior during copulation.—The female perched on a branch in the soliciting position; the male lowered the tail and anal region and made contact with her cloaca. Four males extended and beat their wings; six left the wings folded. Two males pecked at the female's head or grasped the feathers of her nape with the bill; the others omitted this (compare Marler 1956: 114; see the experiments, p. 56). Copulation lasted 1–12 sec, usually 2–3 sec. In the longest, the female moved some 30 cm with the male on her back; in other cases the female's feet were motionless. Ellen D. Ketterson (pers. comm.) saw a pair copulate three times in 25 sec.

One male sang a Trill while mounted, and the female called Seep three times; another sang a Trill as he left the female. A female Twittered as she solicited and again as she repelled the male briefly before copulation. A third female called Chek afterward. Three copulations were silent. In the case seen by Ketterson, while the male was still on the female's back she turned her head around toward him and they opened and clasped bills.

Copulation took place on perches 0.6–12 m high (mean 6.5 m) and occurred both at margins of territories and in the center. Times were 0630 to 1700, with seven of nine cases before 1200. Dates were 1 May–2 July. Copulation during incubation and care of nestlings is said to be rare among most birds (see p. 229; compare Ficken 1963).

Postcopulatory behavior.—Behavior of males varied as follows: One male immediately tried twice more to mount the female, following her in butterfly flight and evidently succeeding in copulating a second time. Another pursued the female 5 m to the ground, pulled her tail as after sexual chasing and immediately

pursued her out of sight. In a similar case obscured by foliage, a male dismounted after 6 sec and seemed to pull the female's tail while beating his wide-spread wings for 3–4 sec. In other instances males merely hopped away from females, sometimes accompanying them when they resumed activity. The presence of an aggressive tendency in copulating males seems indicated by singing, chasing, and tail pulling.

The postcopulatory behavior of females, in addition to calling and the behavior mentioned above, consisted of sitting motionlessly 2–10 sec, then preening or feeding or gathering nest material. Two females jerked the posterior half of the body sharply up and down several times, flexing the legs and feet; this regularly occurs after defecation (p. 497). Existence of conflicting agonistic motivation in copulating females is indicated by the cases in which males were repelled after being solicited and the cases of females that submitted to tail pulling.

Reverse mounting.—I observed one certain and one probable instance of reverse mounting. In the certain case, a pair whose first nest had failed that morning explored at 1810, the male participating actively and perching in and near forks being inspected by the female. After the male had nest-shaped in one site for 10 sec the female returned and sat beside him, then mounted on his back and stood on him for 2 sec. The male burst into loud song of his preferred group-A version and glided down from the site, in which the female remained. Ficken (1963) saw three cases of reverse mounting by American Redstarts, two in circumstances like those just described. She concludes, "It appears that 'pseudo male' behavior is stimulated by the crouched posture of the male, which resembles the posture assumed by a sexually motivated female. . . ."

In the probable case, the pair had lost a nest to a predator on 25 May. For 13 days the female did not rebuild, instead toying often with nest material and constructing one fragment. The male followed attentively, behaving normally for a male whose female is at the pre-nest-building stage. On 29 May, the pair engaged in mounting for 7 sec, the top bird, almost certainly the female, pecking at the lower one's nape. The circumstance here, i.e. the female's evident inability to build a replacement nest for an unusually long time (see Chapter 14), may have thwarted the aroused sex drive of the male. Sexual frustration is one of the four factors that Morris (1955) regards as a cause of pseudomale and pseudo-female behavior. Long frustration of sex drive may not explain the first, certain case of reverse mounting; but if male nest shaping is viewed as a "releasing stimul[us] for the sexual behaviour of the opposite sex" (Morris 1955: 49), the female's pseudomale behavior can be attributed to another of the causes of inversion suggested by Morris.

Other inversion.—Other male behavior apparently appropriate to the opposite sex will be noted here for convenience but described in connection with the stages of the reproductive cycle at which it occurred. A male encountering a neighbor male assumed the female soliciting posture (see p. 44). Males may have engaged in the solicitation posture and directed it at females carrying food to nestlings (p. 283). Note also male nest-shaping and related behavior, described above.

CHAPTER 13

THE TIMING OF THE BEGINNING OF NESTING

PAIRS FORMED AT BEGINNING OF SEASON

The pairing-to-building period at the beginning of the season (p. 89) began on the day the female joined her eventual mate and ended at the close of the day before she started her first nest. This combining of the pair-formation period with the pre-nest-building period, which is contrary to common practice, is necessary because in the Prairie Warbler there was no objective dividing line between those two stages. The population nest-starting interval began each year on the day the first female commenced building and ended with the close of the day before the last female commenced building at the beginning of the season.

I knew the dates on which 121 pairs formed and on which the females of these began their first nests.

Dates; nest-starting interval.—Table 27 presents the dates on which building the first nest began during 14 years. For 9 years in which at least five females were studied, it also shows the durations of the population nest-starting interval and of the interval in which approximately the middle 66% of the females began to build. The earliest date on which the year's first nest was begun was 25 April, the latest was 6 May, and the mean was 30 April–1 May. The earliest date on which the last female to build began her first nest was 6 May, the latest was 24 May, and the mean for the years with at least five cases was 13–14 May. The nest-starting interval varied from 9 to 22 days; the mean was about 15 days. The duration of the interval in which the middle 66% of the nests were started ranged from 4 to 18 days; the mean was about 9 days.

Dates according to age of females.—The dates on which 35 yearlings and 78 females older than 1 year started to build were sufficiently evenly distributed among the years to permit direct comparison of calendar dates. The mean for the older birds was 6.0 May (SD 4.8 days) and for the yearlings 8.3 May (SD 5.9 days); $t = 2.19$; $df = 111$; $P < 0.05$. This difference of about 2 days corresponds approximately to the difference in migration schedules and pairing dates of the two age classes (see Chapters 3 and 11). Tests designed to reveal whether other factors (age of male, nature of territory, etc.) might also be involved were negative, and I conclude that yearling females began to build a little later because they arrived and paired a little later.

Pairing-to-building period.—Table 28 distributes 121 pairing-to-building periods by length, showing also the ages of the females, to be discussed below. Extremes were 0 days (the female began to build the day she paired) and 15 days; the mode was 2 days and the median 4.2 days; the mean was 5.0 days (SD 3.6 days). Table 29 presents statistics on pairing-to-building periods according to year.

Relationship between date of pairing and pairing-to-building period.—Table 30 presents correlation and regression analyses of length of pairing-to-building period on relative date of pair formation for the 121 cases pooled and also for annual

TABLE 27
DATES OF BEGINNING OF BUILDING OF FIRST NESTS, 1952-1966¹

	Number of females	Earliest date	Period of beginning middle 66% ² of nests		Latest date	Mean date	Length of population nest-starting interval ³ in days
			Extreme dates	Duration in days			
1952	4	30/4	—	—	—	—	—
1953	3	4/5	—	—	—	—	—
1954	5	25/4	26/4-3/5	8	11/5	30/4	17
1956	2	6/5	—	—	—	—	—
1957	3	30/4	—	—	—	—	—
1958	19	3/5	5/5-12/5	8	14/5	9/5	12
1959	16	1/5	2/5-9/5	8	14/5	5/5	14
1960	14	26/4	27/4-14/5	18	16/5	3/5	21
1961	15	3/5	5/5-16/5	12	24/5	12/5	22
1962	14	2/5	4/5-11/5	8	13/5	6/5	12
1963	10	26/4	6/5-9/5	4	11/5	6/5	16
1964	9	28/4	30/4-5/5	6	6/5	1/5	9
1965	2	2/5	—	—	—	—	—
1966	5	5/5	8/5-12/5	5	13/5	10/5	9

¹ Dates were uncertain in 1955.

² The percentage is in most years approximate.

³ See definition, page 110.

subsamples from years with at least nine cases. All regression coefficients but one are negative. However, even though females that paired earlier tended to wait longer before beginning to build, the longer wait did not cancel out the effect of early pairing. That is, in none of the 7 years was the regression coefficient greater than -0.42, and for the pooled data it was only -0.12. Therefore, pairs that formed

TABLE 28
DURATION OF FIRST-NEST PAIRING-TO-BUILDING PERIODS¹ OF 121 FEMALES, ACCORDING TO AGE OF FEMALE

Duration in days	Old females	Yearling females	Females of unknown age	Totals
0	1	0	0	1
1	7	3	2	12
2	12	5	7	24
3	11	2	0	13
4	6	2	7	15
5	10	3	2	15
6	11	1	3	15
7	1	0	2	3
8	4	2	1	7
9	1	0	0	1
10	1	3	0	4
11	2	0	0	2
12	2	0	2	4
13	0	0	0	0
14	1	0	2	3
15	0	0	1	1
16	0	0	0	0
17	1	0	0	1
Totals	71 ²	21 ³	29	121 ⁴

¹ The pairing-to-building period of the first nest is defined on page 110. Only pairs formed at the beginning of the season (see page 89) are considered.

² The mean is 4.8 days (SD 3.3 days), the median 4.3 days.

³ The mean is 4.5 days (SD 3.1 days), the median 3.8 days.

⁴ The mean is 4.9 days (SD 3.6 days), the median 4.2 days.

TABLE 29
DURATION OF FIRST-NEST PAIRING-TO-BUILDING PERIODS,¹ ACCORDING TO YEAR

	Females, N	Duration in days		
		Shortest	Longest	Mean ²
1952	4	2	5	(3.5)
1953	3	2	5	(3.7)
1954	5	2	12	5.0
1956	2	5	7	(6.5)
1957	3	4	14	(7.3)
1958	19	2	14	6.2
1959	16	1	10	3.4
1960	14	0	8	3.3
1961	15	2	15	6.8
1962	14	2	6	3.4
1963	10	1	11	4.3
1964	9	1	8	3.8
1965	2	6	12	(10.5)
1966	5	5	17	8.5

¹ The pairing-to-building period of the first nest at the beginning of the season is defined on page 110.

² Means of fewer than five cases are in parentheses.

earlier also tended to begin building earlier; and the chances of having a longer nesting season were greater for females that paired early, with the probable advantages discussed on page 93; see also page 188.

Influence of development of vegetation on beginning of nesting.—The state of the vegetation when females arrived and paired was given considerable attention for its possible effect on the timing of nesting, but I could find no evidence that annual differences in development of vegetation (qualitative evidence as well as analysis of temperature) were associated with variation in timing of building. Leafy potential nest sites were always available at time of arrival, because of the presence on all territories of Red Cedar and/or pines as well as tangles of Japanese Honeysuckle (see p. 134). Similarly, within each year the state of the vegetation on the various territories had no apparent effect on the promptness with which building began. Vegetational differences existed among territories (Chapter 29), but these were not correlated with dates of nest building.

Influence of air temperature on beginning of nesting.—Because pairs formed on

TABLE 30
CORRELATION AND REGRESSION ANALYSES¹ OF LENGTH OF FIRST-NEST
PAIRING-TO-BUILDING PERIOD² AND DATE OF PAIR FORMATION

	df	Coefficient of correlation (r)	Regression coefficient	t
All years pooled	119	-0.18	-0.12	-1.96
1958	17	-0.56	-0.39	-2.77
1959	14	-0.15	-0.13	-0.58
1960	12	0.35	0.17	1.31
1961	13	-0.40	-0.29	-1.59
1962	12	-0.68	-0.24	-3.24
1963	8	-0.44	-0.30	-1.40
1964	7	-0.89	-0.42	-5.17

¹ Years in which fewer than nine data were available were not analyzed separately.

² The pairing-to-building period of the first nest at the beginning of the season is defined on page 110.

TABLE 31
RELATION BETWEEN MEAN TEMPERATURE AND BEGINNING OF NEST
BUILDING ON RAINLESS DAYS

Mean temperature on day building began, relative to ¹ normal mean ² for day	Female days of exposure ³	Females that began to build	
		N ⁴	% ⁵
over 8.6° +	31	10	32
8.6° - 5.9° +	31	16	52
5.8° - 3.1° +	56	15	27
3.0° - 0.3° +	71	21	30
0.2° - 2.4° -	44	12	27
2.5° - 5.2° -	50	8	16
5.3° - 8.0° -	29	2	7
over 8.0° -	6	0	0
Totals	318	84	

¹ Differences are in degrees C.

² Normal means for Bloomington are recorded in Visser (1944: 476).

³ See text, this page.

⁴ Number of females that began to build the first nest on days with the indicated temperature.

⁵ The percentage is derived by dividing the number of female-days of exposure into the number of females that began to build.

different dates and began nesting on different dates, analysis of effect of air temperature must isolate each pair's pairing-to-building period. To summarize such analysis, I use the concept of female-days of exposure: Counting only rainless days (i.e. calendar dates), I checked all days on which at least one paired female that had not begun to build was present on the study area. If three paired females without nests were present on a particular date, that date produces 3 female-days of exposure to the temperature that prevailed. I then calculated the mean temperature for each day, compared each such mean with the normal (long-term) mean for the day (Visser 1944: 476), distributed female-days of exposure according to unit-intervals of temperatures deviating from long-term means, and tabulated numbers of females, relative to female-days of exposure, that started to build at various deviations from mean temperatures.

Table 31 indicates that temperatures 2.5°C or more below normal retarded beginning of building. In a test of independence of the data in the table, Chi-square = 23.9; df = 6; $P < 0.001$. Data for temperatures more than 5.2°C below normal were pooled because of small numbers.

Considering only days whose means were 2.5°C or more below the long-term mean, on 13 such cold dates no female started a nest and on 9 one or more females did start. Now comparing these 13 and 9 days, differences between them become apparent. High temperatures on the 9 days on which building began averaged 20.0°C but on the 13 days on which building did not begin, 14.7°C, a difference of 5.3°C. Low temperatures on the two groups of days averaged 3.9°C and 2.2°C, respectively, a difference of only 1.7°C. Inasmuch as daily minimum temperatures in spring usually occur at night, it can probably be said that the daytime temperatures on the 9 days building began were not in fact as cool as the daily means would indicate; this underlines the inhibiting effect of low daytime temperature on start of nesting. A rough idea of the approximate threshold temperature necessary for females to begin building is suggested by Table 32; 17.2°C was the lowest maximum (therefore, probably daytime) temperature for

TABLE 32
MAXIMUM AIR TEMPERATURES ON COOL¹ DAYS ON WHICH FEMALES
DID AND DID NOT BEGIN TO BUILD FIRST NESTS

	Maximum air temperature			Totals
	21.1°C or above	21.0°C–17.2°C	17.1°C or below	
Days on which building began	4	5	0	9
Days on which no building began	0	2	11	13

¹ A day is regarded as cool if the mean air temperature was at least 2.5°C lower than the normal mean for that date.

any day on which a first nest was begun. No independent effect of minimum (probably night) temperature was detected.

Nothing suggests that females had to experience any accumulation of warm days after pairing before they began to build. (Use of female-days of exposure presupposes the female's response to temperature on any day is independent of the temperature of the day before.) For example, in several years considerable numbers of birds (e.g. seven) started nests within 1–2 days, although they had been present for varying intervals and therefore subjected to different weather in the immediate past. Further, some females began to build within 1–2 days of pair formation, before experiencing any accumulation of warm days after pairing.

In one respect temperature on the day preceding beginning of building appeared important, as suggested by several episodes. A number of times, several females simultaneously started building on a day of rising temperature following a cold and sometimes rainy period, making it seem likely that females responded to the warming trend. In Indiana as in much of the northeastern United States, alternations of warm and cool periods are frequent in April and May, with several days of warm weather often following a cool spell. An immediate response to rising temperature would usually permit a female to complete her nest in warm weather (see Chapter 17 for the time required to build nests).

I detected no tendency for females to begin building at lower temperatures as the date advanced, i.e. no lowering threshold. For example, I divided the period 26 April–15 May (1954, 1958–1964) into 5-day intervals, obtained the maximum temperature for each day, and calculated the mean daily maximum for each 5-day interval and the mean daily maximum for only those days on which females

TABLE 33
MAXIMUM TEMPERATURE ON DAYS WHEN FIRST NESTS WERE BEGUN,
ACCORDING TO ADVANCING DATE

	Nests begun	Mean of maximum temperatures during study ¹	Maximum temperatures on days females began nests ¹		
			Highest	Lowest	Mean
26–30 April ²	13	22.3	30.6	17.2	25.0
1–5 May	36	23.7	33.9	18.3	26.5
6–10 May	22	22.3	33.3	17.2	26.7
11–15 May	26	24.2	32.2	17.8	25.8

¹ Years are 1954 and 1958–1964. Temperatures are in degrees C.

² One nest was begun on 25 April.

TABLE 34
NESTS BEGUN ON DAYS CLASSIFIED ACCORDING TO AIR TEMPERATURE
AND RAINFALL

Weather ¹	Number of days of exposure of paired females ²	Females beginning nests	
		N	%
Hot-dry	147	53	36
Hot-rainy	22	5	23
Cool-dry	172	31	18
Cool-rainy	99	12	12
Very rainy	30	1	3
Totals	470	102	

¹ A day was hot if the maximum temperature was at least 25°C; other days were cool. A day was very rainy if at least 25 mm of rain fell during the 24 hours, rainy if less than 25 mm of rain but more than a trace fell before 1500; other days were dry.

² Each female that had been paired at least 1 day but had not begun to build is counted as 1 for each day on which she was exposed to the weather indicated.

began to build. Table 33 reveals that, on the average, females began to build on the warmest days of the various 5-day periods and shows no tendency to start to build at lower temperatures as the date advanced. This is well illustrated by the data from 6–10 May, an interval that in the years in question was cooler than the preceding 5-day interval and as cool as the last 5 days of April. Yet the mean maximum temperature at which females started building was as high as or higher than that of the two preceding periods, not lower.

Influence of rainfall, clouds, and wind on beginning of nesting.—In 1954 and 1958–1964, measurable rain on dates and at times of day relevant to beginning of building first nests fell on 42 days. Because females were never known to begin a nest after 1500 in any weather (p. 149), days on which it rained only after 1500 were not classed as rainy. Each day on which at least one paired female had not begun to build is assigned to one of the following categories: very rainy (at least 25 mm rainfall), hot-dry (maximum temperature at least 25°C, no rainfall), hot-rainy (at least 25°C, measurable rainfall less than 25 mm), cool-dry, and cool-rainy. The point 25°C is used because the mean maximum temperature on days when first nests were begun was 25°C or slightly higher. There were too few (8) very rainy days to classify these according to air temperature.

Table 34 distributes female-days of exposure (calculated as on p. 113) of paired females that had not yet begun to build among the five weather categories, showing numbers and percentages of birds that started nests. The proportion of nests started was lower on rainy than on dry days within each temperature subcategory and fewest nests were begun in very rainy weather, suggesting that rain had an inhibiting effect independent of temperature. However, results of tests of independence of the data from the hot-dry and hot-rainy subcategories and of data from the cool-dry and cool-rainy subcategories are nonsignificant.

Beginning of building seemed to be unaffected by cloud cover or by normal winds for April and May (southwest at 10–20 knots).

PAIRS FORMED IN MIDSEASON

The pairing-to-building period of females that paired in midseason (defined on p. 89) was measured as was the period at the beginning of the season. I

knew both dates of pair formation and of beginning of building for 20 pairs in which the female appeared on a territory that the male had held all season. Most, possibly all, females had nested previously that season (see Chapters 30 and 31), and all males had; two females had nested earlier on the study area.

Dates.—The dates on which building began in the 20 cases ranged from 18 May to 8 July. Three dates fell in May and three in July; the rest in June.

Pairing-to-building period.—The lengths of the 20 periods were 0 days, 3 cases; 1 day, 5 cases; 2 days, 10 cases; 4 days, 1 case; 9 days, 1 case. The mean is 1.9 days (SD 1.9 days).

These pairing-to-building periods in midseason were about as brief as replacement periods of females that renested without changing mates (Chapter 14) and were much shorter than pairing-to-building periods at the beginning of the season. Females in these midseason pairs may have been physiologically more ready to nest when they joined males (e.g. they had not just completed the migration), and none of them experienced cool or prolonged rainy weather after pairing.

The three cases of birds that began to build on the day of pair formation all fell late in the season (24 June and thereafter). The female that took 4 days to begin to build paired on 22 May, and the one that took 9 days (during which she built one fragment) paired on 23 May. The fact that the only two long periods were in May suggests that possibly these two females were late migrants and that their long periods preceded the first nest.

CHAPTER 14

THE PRE-NEST-BUILDING PERIOD OF REPLACEMENT AND SECOND-BROOD NESTS

REPLACEMENT NESTS

A replacement nest was built after most failures. The pre-nest-building period, i.e. replacement period, began when the prior nest failed and ended with the close of the day before the replacement nest was started; a fraction of a calendar day is counted as a whole. When nests failed at night, the replacement period started the following morning. Many nests failed between two inspections 24 hours apart. These are excluded, and the sample consists of 202 cases in which failure could be assigned with considerable assurance (because of timing of inspections or other special circumstances) to a specific day. The 202 periods involved 116 individual females.

When eggs or nestlings disappeared piecemeal over the course of several days, the nest is considered to have failed when the last of its contents disappeared unless there is evidence that the female deserted earlier. Females never deserted nests as long as a nestling remained; promptness of desertion after piecemeal predation of eggs varied.

Length of replacement period.—As Table 35 shows, seven females started to rebuild on the day of failure, thus having replacement periods of 0 days. The longest period was 14 days; the mean was 1.7 days, the median 1.2 days. Most replacement nests (67%) were begun the day following failure.

Stage at which predecessor nests failed.—Table 35 distributes the 202 replacement periods by length, according to the stage at which the predecessor nest failed. Six stages of reproduction are distinguished and defined in the table. As is evident, replacement periods did not differ in length according to stage of the predecessor nest at failure. The Prairie Warbler therefore deviates from what is said to be a common avian pattern of delaying replacement longer, the more advanced the stage of reproduction in the previous nest (see Verner 1963).

Date on which predecessor nest failed.—Table 36 distributes the replacement periods among 10-day calendar intervals, except that the last interval is longer, according to date of failure of the predecessor nest. There is no statistical evidence of variation.

Number of previous nest failures of individual female.—To investigate whether a female's earlier experiences in the same season might affect the speed with which she started a replacement nest, I selected only those 173 nests built by females (105 individuals) whose complete previous reproductive histories of the season I knew (Table 37). Birds that paired late were the principal group eliminated. Again, there is no statistical evidence of variation. One female supplied eight cases of replacement in one season. After several of her early nests failed, I began to take her new nests as soon as laying was completed. All her replacement nests were begun on the day following failure, with the exception of her sixth and eighth replacements. She started these in the early afternoon

TABLE 35
LENGTH OF REPLACEMENT PERIOD,¹ ACCORDING TO STAGE OF REPRODUCTION
OF PREDECESSOR NEST AT FAILURE

Replacement period, days	Stage of prior nest at failure						Total (all stages)
	Active building ³	Inactive building ³	Laying ⁴	Early incubation ⁵	Late incubation ⁶	Nestling ⁷	
0	3	0	1	3	0	0	7
1 ²	10(67%)	5(71%)	31(62%)	54(70%)	19(73%)	17(63%)	136(67.3%)
2 ²	1(1%)	0	12(24%)	8(10%)	4(15%)	4(15%)	29(14.4%)
3	1	1	1	6	2	3	14
4	0	0	1	1	0	1	3
5	0	1	3	1	0	1	6
6	0	0	1	1	0	0	2
7	0	0	0	1	0	0	1
8	0	0	0	1	0	0	1
9	0	0	0	1	0	1	2
14	0	0	0	0	1	0	1
Totals	15	7	50	77	26	27	202
Median	1.0	1.2	1.3	1.2	1.2	1.3	1.2
Mean	1.0	1.9	1.7	1.7	1.8	1.9	1.67
SD	0.8	1.6	1.3	1.6	2.6	1.8	1.66

¹ The replacement period is defined on page 117. If a nest was begun on the day its predecessor failed, the period is 0 days.

² Numbers in parentheses show percentages of 1-day and 2-day replacement periods among total periods following failures at the indicated stages; total periods, medians, means, and standard deviations are shown below.

³ Phases of building are defined on page 149.

⁴ The laying interval began with the laying of egg 1 and ended with the laying of the final egg.

⁵ For purposes of this table, the early incubation period began with the laying of the final egg and ended 6 days later.

⁶ For purposes of this table, the late incubation period began with the end of the early incubation period and lasted through the day on which hatching began. This period was 5-6 days long.

⁷ For purposes of this table, the nestling interval began with the start of hatching and lasted till all young left the nest. This period was 8-11 days long.

TABLE 36
LENGTH OF REPLACEMENT PERIOD,¹ ACCORDING TO DATE OF FAILURE OF
PREDECESSOR NEST

Replacement period, ¹ days	Date of failure						Total (all stages)
	6 May-15 May ³	16 May-25 May	26 May-5 June	6 June-15 June	16 June-25 June	26 June-19 July	
0	2	0	0	2	2	1	7
1 ²	16(64%)	32(73%)	19(56%)	26(59%)	19(79%)	24(77%)	136(67.3%)
2 ²	4(16%)	7(16%)	4(12%)	10(23%)	1(4%)	3(10%)	29(14.4%)
3	0	1	8	3	1	1	14
4	0	1	0	1	0	1	3
5	3	1	1	0	0	1	6
6	0	0	0	1	1	0	2
7	0	1	0	0	0	0	1
8	0	1	0	0	0	0	1
9	0	0	1	1	0	0	2
14	0	0	1	0	0	0	1
Totals	25	44	34	44	24	31	202
Median	1.2	1.2	1.4	1.3	1.0	1.1	1.2
Mean	1.6	1.7	2.3	1.7	1.3	1.4	1.7
SD	1.4	1.5	2.6	1.5	1.3	1.1	1.3

¹ The replacement period is defined on page 117. If a nest was begun on the day its predecessor failed, the period is 0 days.

² Numbers in parentheses show percentages of 1-day and 2-day replacement periods among total periods following failures at the indicated stages; total periods, medians, means, and standard deviations are shown below.

³ Included is one nest that failed prior to 6 May.

TABLE 37
LENGTH OF REPLACEMENT PERIOD,¹ ACCORDING TO NUMBER OF NEST
FAILURES² PREVIOUSLY EXPERIENCED BY FEMALE³

Replacement period, ¹ days	Number of previous nest failures ²								Total
	1	2	3	4	5	6	7	8	
0	0	1	0	1	0	1	0	1	4
1 ⁴	46(64%)	35(69%)	23(72%)	8(73%)	3(100%)	1(50%)	1(100%)	0	117
2 ⁴	12(17%)	9(18%)	5(16%)	1(9%)	0	0	0	0	27
3	5	4	0	1	0	0	0	0	10
4	1	0	2	0	0	0	0	0	3
5	4	0	1	0	0	0	0	0	5
6	0	1	1	0	0	0	0	0	2
7	1	0	0	0	0	0	0	0	1
8	1	0	0	0	0	0	0	0	1
9	1	1	0	0	0	0	0	0	2
14	1	0	0	0	0	0	0	0	1
Totals	72	51	32	11	3	2	1	1	173
Median	1.3	1.1	1.2	1.1	—	—	—	—	1.2
Mean	2.0	1.6	1.6	1.2	—	—	—	—	1.7
SD	2.2	1.4	1.3	0.8	—	—	—	—	1.7

¹ The replacement period is defined on page 117. If a nest was begun on the day its predecessor failed, the period is 0 days.

² In this table a failure is the loss of a nest at any stage, beginning with building. The number of nest failures is the number experienced by the individual in the year in which the replacement period was observed.

³ Data are taken from 105 females.

⁴ Numbers in parentheses show percentages of 1-day and 2-day replacement periods among total periods following failures at the indicated stages; total periods, medians, means, and standard deviations are shown below.

of the days on which (at 1200 and 1100, respectively) I had taken their predecessors. (After the loss of her eighth replacement nest on 12 July she remained for two days with her mate, which courted her; she then disappeared. Because it was unusual for females to stay on territories more than a few hours after nest failure unless they were going to rebuild, this female probably experienced some motivation to build another replacement but was unable to do so.)

Air temperature.—Low air temperatures were rare at dates on which temperature might influence the start of building, and statistical evidence on this point is lacking. A female once began a replacement nest when the maximum temperature was 13.9°C (and continued next day when the maximum was 10.0°C). This was the lowest temperature at which nest building started during the study.

Rain.—Indications are that rain tended to inhibit the beginning of building of replacement nests. To analyze this question days are classed as rainy or dry using the method described on page 115. In an effort to eliminate motivational differences not associated with rain, consideration is restricted to females whose nests failed no later than 15 June and whose replacement periods did not exceed 2 days. The question is whether the day following failure was rainy or dry and whether the female did or did not begin to rebuild on that day. There are 115 cases (see Table 38). On 36 rainy days, 23 females did and 13 did not begin to rebuild. On 79 dry days 68 females did and 11 did not begin to rebuild. In a test of independence, adj. Chi-square = 6.1; df = 1; $P < 0.025$. In 9 of the 13 instances in which females skipped a rainy day and then started to build, the day of building

TABLE 38
FREQUENCY OF 1-DAY AND 2-DAY REPLACEMENT PERIODS,¹ ACCORDING TO
WHETHER RAIN FELL ON DAY FOLLOWING FAILURE OF PREDECESSOR NEST

Length of replacement period ¹	Cases, according to weather on day following nest failure		Totals
	Rainy ²	Dry ²	
1 day	23	68	91
2 days	13	11	24
Totals	36	79	115

¹ The replacement period is defined on page 117. Nests that failed after 15 June are excluded.

² A day is rainy if there was more than a trace of rain and if it began to fall before 1500. All other days are dry.

was not rainy. Some of the strikingly long replacement periods occurred in spells of rainy weather.

Consistency in replacement periods of individual females.—For 25 females I know the lengths of three or more replacement periods and these provided some suggestion that individuals tended to be consistent in length of period. Seven females invariably began to replace nests on the day following failure. Six others differed only in that all their periods were 0 and 1 or 1 and 2 days long. The remaining 10 females behaved less consistently; the lengths of their replacement periods were never the same or those deviations that occurred were greater than 1 day. However, 4 of these 10 females exhibited another sort of consistency: more than once they had unusually long periods (4 and 5 days, 9 and 6 days, both 3 days, and both 3 days).

Of the 202 replacement periods in the sample, only 30 (15%) were 3 days or longer; 5 females (4%) from the 116 individuals whose periods were analyzed had 2 such long periods in a single season. Rain does not account for these cases.

Periods between desertion of unused nests and beginning of replacements.—Occasionally nests were completed, never used, and replaced (see p. 185). These nests were excluded from the sample considered to this point, because dates of failure are unascertainable. However, in 11 instances I know the number of days between completion of the unused nest and beginning of the replacement: extremes are 2 and 12 days, the mean 7.5 days. The 2-day period is an unusual case: In bad weather a female took 11 days to build the first nest, about three times longer than normal (see Table 36). Two days after finishing it, when laying would be expected, she began another nest. Disregarding this instance, the shortest period of the kind being considered was 4 days and the mean was 8 days.

SECOND-BROOD NESTS

The pre-nest-building period of second-brood nests began the day the first brood left the nest and ended with the day before the female started the second-brood nest. The definition excludes periods required to replace second-brood nests that failed, a few of which are described on page 121.

Because of the low rate of success of nests built early in the season (p. 398), few females had time to attempt a second brood. In the 18 cases to be analyzed, 15 females built and laid in second-brood nests without changing mates, one fe-

male without changing mates built but did not lay in a second-brood nest, and two females changed mates before building and laying.

The pre-nest-building period.—Fourteen pre-nest-building periods are known with a margin of error no greater than 1 day. Extremes were 1 and 26 days, the mean 9.6 days (SD 4.0 days). Six of these periods were 7–9 days long. If three additional cases with margins of error no greater than 2 days are added to the 14 above, the mean is lengthened to about 10 days.

One of the two instances of females that changed mates is included in the cases just analyzed and one is not. In the included case the female abandoned her initial brood a few hours after they left the nest on 5 July, joined her mate of the preceding year, and began a nest. The excluded female began a second-brood nest about 36 days after her first brood left the nest, but I am not sure that she had made no earlier second-brood attempt.

Date and length of pre-nest-building period.—The considerable variability in length of the pre-nest-building period of second-brood nests may have been related, at least in part, to the date at which the first brood left the nest, as the following suggests: Of the 17 periods with margins of error no greater than 2 days, 8 involved females whose first brood left the nest before 10 June; 9 involved females whose broods left after that date. The mean of females that brought off young before 10 June was 15 days as compared to 6 days for females that succeeded later.

Size of first brood and length of pre-nest-building period.—Length of the period may have been affected by size of the first brood; larger broods perhaps required the attention of both parents for a longer time. Of the 16 cases in which brood size was known, four females that brought off two young averaged 6.5 days before beginning to build again; six females that brought off three young averaged 4.5 days; six females that brought off four or (in one instance) five young averaged 16.0 days. Two females produced one fledgling apiece (a cowbird in each case) on dates early enough to lead me to expect a second-brood attempt, but each disappeared on the day the fledgling left the nest. These females may have died, but more likely they abandoned their males and young (see p. 346) and sought new mates.

Replacement periods of second-brood nests.—Ten females that built nests and laid eggs for second broods lost the nests to predators; the others succeeded. Four of the 10 that failed built replacement nests, and 6 quit nesting for the year. Of those that renested, 2 did so the day following failure, 1 after a wait of 1 day, and 1 after a wait of 3 days.

CHAPTER 15

THE NEST AND ITS SITE

THE NEST

General description.—Nests consisted of an outer shell, padding, and a lining. These usually differed in composition and construction, but the transition from one part to another was never abrupt. A basal wad, a mass of material attached sometimes loosely to the bottom of the outer shell, was also present on some nests. Nest placement was of the attached-stantant type (Berger 1961: 217–218). Most attachments to the nest plant were spider webs, but long plant fibers were at times woven around supporting branches and twigs. All but two or three nests were cup-shaped (Figs. 10 and 11). Cups were compact and of about equal width and height, usually slightly constricted at the rim.

The general exterior color was a composite of brownish olive, olive, and medium gray (Palmer 1962: chart at 4). The interior was most often buffy brown, but some lining materials produced striking departures, e.g. black (cow hair) and brownish red-scarlet orange (rootlets of moss).

The exterior texture was soft and at times slightly shaggy. A lateral pattern or grain resulting from the position in which the materials were inserted was visible from the rim to about halfway down the sides; below that point most fibers had been laid in all directions. Insect and spider egg cases, pieces of snakeskin up to 15–20 cm long, woolly seeds, and pieces of soft paper were sometimes present on the outside. Usually the lining showed no grain.

Outer shell.—Webs cemented together plant fibers of two kinds: soft, pliant, bast (often milkweed or fleabane) usually 8–12 cm long and about 3 cm wide; and short, stiff, bark-like pieces of epidermis. Other materials in outer shells were pieces of dead leaves, dead grass blades and inflorescence stems, and materials mentioned in the preceding section. Stiff fibers usually were inserted after a thick cup had been constructed of soft substances; stiff strips were forced into this soft matrix, pushing the walls outward and making them firm and somewhat rigid. Stiff materials also formed the rim of most nests, laid laterally on the top or just inside the top of the wall; the rim was firm and solid.

A soft basal wad of varying size was present on the bottom of about 20% of the nests; some wads weighed 1.3 g (see nest weights, Table 39). At times wads were barely attached appendages. They did not appear to contribute to nest stability and probably were functionless fragments (Chapter 12) on which true nests were built.

Padding.—Downy seeds of Broomsedge were the principal padding in many nests; down from fruits of pussy's toes was much used in May and early June. Also important were down of milkweed, fleabane, thistle; woolly masses surrounding seeds of thimbleweed; feathers of birds; fur of various mammals; and parts of grasses. Soft brown fibers from Sycamore fruits as well as pieces of green moss were used occasionally. One nest contained some 250 feathers of a Mourning



FIGURE 10. Three common kinds of nest placement. From left to right are placement types I, II, and III; see text. Photographs were taken in early spring of the year following the one in which the nests were built.

Dove, another many from a male Cardinal. One builder inserted many Starling feathers in all four of her nests one year. Some females used one padding material almost exclusively; other females relied on a mixture. There was no regular arrangement; items simply were packed together. Padding was thickest on the bottom of the cavity (typical layer 9 mm thick); in some nests it extended up the sides to the rim but in others was almost confined to the bottom. Occasionally nests had almost no padding.

Lining.—Commonest substances were axes of inflorescence of grasses, especially Purpletop. Some linings were predominantly of fur or feathers. Plant down, grass, leaves, and occasionally tiny rootlets and spore capsules of mosses pulled alive from the ground were used (compare Bagg and Eliot 1937: 569). Lining was thickest on the bottom of the nest; many nests were almost unlined on their vertical walls.

Materials used in other localities.—Examination of nests from other parts of the range and of written descriptions shows little geographical variation. Materials used in limited parts of the range are shreds of palmetto fiber (Florida race, A. H. Howell 1932: 409), bark of cedar trees (Coues 1888), pine needles (South Carolina, Sprunt and Chamberlain 1949: 469), willow catkins and loose cottony material from the inner bark of old Jack-Pines (Michigan, Walkinshaw 1959), and cotton (Georgia, Burleigh 1958: 540). Coues (1888) describes nests chiefly of white dandelion down (one colorfully lined with red cow hair) and of cotton

TABLE 39
WEIGHTS OF NESTS AND THEIR PARTS

Weights ¹	N	Extremes	Mean	SD
Complete nests				
All nests	90	7.3–2.4	4.2	1.0
First nests of season ²	39	7.3–2.4	4.6	1.1
Replacement nests ²	38	5.2–2.5	3.8	0.7
Outer shell ³	41	4.4–1.2	2.6	0.7
Padding-lining ³	41	3.5–0.6	1.7	0.6
Lining ³	14	1.6–0.2	0.5	0.4

¹ Weights are in g.

² Sequence of some nests was unknown.

³ See pages 122 and 124.

TABLE 40
DIMENSIONS¹ OF NESTS

	N	Extremes	Mean	SD
Diameter at rim				
External	68	73-50	60.1	5.0
Internal	67	51-36	42.1	2.9
Diameter 15 mm below rim				
External	43	70-55	63.0	4.1
Internal	50	53-38	44.8	3.2
Depth				
Rim to exterior of bottom	68	74-47	59.7	5.8
Rim to interior of bottom	68	45-26	38.1	4.1
Thickness of wall				
At rim	66	14-5	9.4	2.0
15 mm below rim	28	13-6	10.2	1.9
Thickness of floor	66	40-12	21.2	5.4

¹ Measurements are in mm. See text, this page, for methods.

presumably discarded by man. Bailey (1913: 304) refers to nests of sheep's wool; see also Pearson *et al.* (1919: 298).

Nest dimensions.—Surfaces were not smooth, and no nest was perfectly symmetrical; measurements, especially exterior measurements, are therefore approximate. I ignored small irregularities and thin spots and attempted to find means of several diameters of the cavity, walls, etc., of each nest. Insubstantially attached basal wads were ignored.

Exterior and interior diameters were measured both at and 15 mm below the rim. Exterior depth was measured between the rim and a flat surface on which the nest rested upright. Cavity depth was measured between the center of the floor (interior) of the cavity and the plane of a flat object lying horizontal on the rim. Thickness of walls and floor was measured both by subtracting interior from exterior measurements and by pushing a wire through the walls and reading markings on the wire. Measurements of thickness of walls were made at and about 15 mm below the rim of the floor at the center of the cavity.

Table 40 requires little comment. The usual wall thickened slightly progressing from top to bottom, and the floor was more than twice as thick as the wall at the rim. As evidence of the thickness and density of the lower wall and floor, nests left uncovered during heavy rains often held water 5-6 mm deep for 2-3 hours. Seasonal variation in nest dimensions will be discussed in connection with weights, which are more accurate.

Two among about 800 nests that I saw were broad, shallow, and saucer-shaped rather than cup-shaped. One measured 70 mm in external diameter at the rim and only 48 mm in external depth. The materials with which this latter was made were also abnormal in that they were almost all stiff.

Nest weights.—Weights of parts are approximate because the transition between parts was not a clear one. Separation of padding and lining was difficult; only a few lining weights were obtained, and the padding-lining was treated as a unit in most cases. All nests were weighed in winter after storage in dry conditions.

As Table 39 shows, weight of the padding-lining was considerably more variable than that of the outer shell; the few data on the lining alone indicate much variation in that component. I determined the percentages of total weight contributed by the padding-lining of 46 nests. The greatest was 58%, the smallest 18%, the mean 38% (SD 9%). There was no correlation between a nest's total weight and the percentage assignable to the padding-lining.

Walkinshaw (1959) reports weights of three nests from Michigan as 4.2, 6.4, and 7.1 g. The last two of these are unusually heavy compared with my weights, but Walkinshaw may not have dried his specimens before weighing.

Nest weights, according to date.—In a test of significance of the difference in mean weights of first nests of the season and replacement nests (Table 39), $t = 3.80$; $df = 75$; $P < 0.001$. I also tested matched pairs of first and second nests built by 17 females in single seasons. Mean weight of the first nests was 4.9 g, of the second nests 3.9 g; $SD = 1.17$ g; $t = 3.89$; $df = 16$; $P < 0.001$. Weights of second and later nests did not differ.

Materials in first and later nests seemed not to differ; first nests simply contained more material. Their greater bulk probably provided better insulation at the beginning of the season, when temperatures were lower (compare Ricklefs and Hainsworth 1969, Smith *et al.* 1974). An advantage of better insulation is suggested by the fact that cold weather sometimes prolonged the incubation period (p. 236) and therefore the period of vulnerability to predators.

Nest weights according to age of female.—Comparison of weights of first nests of females older than 1 year and yearlings showed no significant difference; the same was true of later nests.

Individual differences in nest building.—The mean depth of all cavities measured was 38 mm; extremes were 45 and 26 mm (Table 40). Following are depths of cavities of sets of two or more nests, each set built by one female. A semicolon separates measurements of one individual's nests from those of the next; for each female, data are presented in the order in which the nests were built: 44, 44; 35, 36; 35, 33, 33; 43, 37; 40, 34, 40, 40; 38, 40, 36; 40, 37; 42, 44, 43; 41, 39, 39; 38, 37; 39, 40; 42, 40, 35; 40, 38; 38, 34. The consistency within most sets suggests individual differences in nest depth, as expected. Diameters of cavities were equally consistent. An episode suggesting individuality in nest construction is this: A female built two nests, so poorly constructed that until eggs were laid I thought they were abandoned fragments; they were less well made than any nests found.

Some females regularly rejected common building materials in favor of a special item seldom used by the majority. For example, one bird used dead leaves of Broomsedge in the outer shell of four nests in preference to the more usual soft bast fibers; her nests were peculiar in texture and color.

PLACEMENT AND SUPPORT

Placement.—Because of the diversity of nest plants and their forms, a completely satisfactory classification of kinds of placement is impossible. The following categories suffice for all but a very few nests (see also Coues 1888, and Walkinshaw 1959). They are assigned Roman numerals for use in later reference.

TABLE 41
PLACEMENT¹ OF 555 NESTS

Placement	Nests	
	N	%
I. In upright fork	260	47
II. Against trunk, on twig(s)	150	27
III. On horizontal or diagonal branch		
a. Small branch	69	12
b. Small, arched tree	22	4
c. Large branch	11	2
IV. In vines	15	3
V. Wedged among small branches	11	2
VI. Fastened to vertical branch(es)	9	2
VII. In broom-like growths	8	1
Totals	555	100

¹ Categories are described in text, this page.

I. In an upright fork, usually formed by three or more branches often about 1 cm in diameter (see Fig. 10-1); in crowns of many tree species, especially small American Elms. Occasionally intersecting branches of different plants formed such forks.

II. Against the trunk of a small tree, resting on little horizontal or nearly horizontal branches and twigs (see Fig. 10-2). The diameter of the trunk typically was 2-5 cm, of the supports beneath the nest 2-15 mm. Many such placements were in American Elms, Sugar Maples, and pines. In elms with Y-forks in the trunk, the nest was often beside or against (not in) the arms of the Y just above their point of origin.

III. On a horizontal or diagonal trunk or branch, usually supported at the sides by twigs or vines. This category can be subdivided into three groups: (a.) On horizontal or diagonal branches having a diameter usually much smaller than the diameter of the nests themselves (see Fig. 10-3). (b.) On trunks of very small trees pulled into a horizontal position by vines or phototropic growth. (c.) On large branches, thicker than the diameter of nests; these solid platforms functioned like nest shelves or ledges.

IV. In a vine, either in a tangle hanging down from a supporting tree or on a thick horizontal stem growing through a treetop.

V. Among and built around a network of crisscrossing and intersecting twigs near the top or periphery of a small tree, e.g. *Crataegus* and *Pyrus* spp., cedars.

VI. Attached to one or more thin upright trunks of small trees or shrubs; no support beneath.

VII. In the center of a tuft-like growth of many twigs, e.g. "witches'-broom" infection of American Hackberry (see Carter 1955: 70-71), twigs of Sassafras, or American Elm.

Placement frequencies according to type.—As Table 41 reveals, 47% of 555 nests for which I recorded the information were located in type-I placements, 27% in type-II, and 18% in type-III. Placement was analyzed according to half-months of the season (not shown), but with one minor exception did not differ according

to date. The exception is that all type-V placements fell in the period ending 15 May. A possible explanation is proposed below, page 129.

Placement by individual females.—Individual females did not use a single type of placement and exhibited no unusual preferences. To illustrate, the following list shows placements of nests of three females that built at least 10 nests. A comma separates nests built in the same year and a semicolon separates years: Female 1: I, III; II, I, II, I, II, VII, I, IV, II. Female 2: I, II, III, III; I, I, I, I; II, I, I. Female 3: II, I, I, I, I; I, II; II; V, I.

Defective placements.—About 15 nests failed or were abandoned because their support was insufficient. Rapid new growth of the nest plant ruined 2 of these; 8 were defectively attached; 4 were fastened only to the side of a single stem (type VI) and gradually sagged with use and growth of nestlings; a nest supported only by pine needles was blown from the tree by wind. A few nests built in upright forks of flexible branches lost one or more eggs when wind tossed the branches.

NEST HEIGHTS

I determined heights of 608 nests, measured from bottom surface to the ground beneath. Most heights were measured directly; those of very high nests were estimated. Table 42 distributes heights according to date and section of the study area, and Table 43 summarizes these data without regard to date.

General.—The lowest nest was 24 cm high, the highest about 13.7 m; 2 such unusually high nests were found. The median height was 1.74 m and the mean 2.29 m (SD 1.89 m). Among 1-m unit intervals, the modal interval was 1–2 m (38%); 77% of all nests were within 3 m of the ground (Table 43).

Heights of Prairie Warbler nests in other localities are reported by Jamison (1889), Daniel (1901), Walkinshaw (1959), Mengel (1965: 418), and Bull (1974: 505; one extraordinary height was 2.5 cm).

Variation according to date.—When the season is divided into 5 periods approximately one-half month long, median height on the Griffey Tract increased from 1.3 m to 2.4 m as the date advanced (Table 42). In an extension of the median test, Chi-square = 44.6; df = 4; $P < 0.001$. On the University Farm the increase was from 1.7 m to 4.8 m. In an extension of the median test, Chi-square = 28.3; df = 4; $P < 0.001$.

Individual females did not always build at progressively ascending heights, of course. Data from two birds that built large numbers of nests illustrate this point: *Case 1*: University Farm, 1957: Nest 1, 1.5 m; 2, 4.6 m; 3, 3.5 m; 4, 3.3 m; 5, 2.0 m; 6, 5.6 m; 7, 4.9 m. *Case 2*: Griffey, 1963: Nest 1, 1.1 m; 2, 3.1 m; 3, 1.5 m; 4, 2.3 m; 5, 2.8 m; 6, 3.5 m; 7, 1.4 m; 8, 8.4 m; 9, 2.5 m.

Seasonally ascending nest heights have been observed in a number of species (see Holcomb and Twiest 1968). Explanations have associated this ascent with variation in concealment as foliage develops (Nice 1937: 92–93) and also with changes in microclimate (Horvath 1964). Microclimatic changes at various heights must have been great, but I have no information about them. On the other hand, data in Chapter 33 show both seasonal differences in intensity of predation on nests at various heights and corresponding shifts in modal nest heights; these point to association between rising nest heights and changing probabilities of

TABLE 42
NEST HEIGHTS,¹ ACCORDING TO SECTION OF STUDY AREA² AND DATE³

Height, m	25 April-15 May				16 May-31 May				1 June-15 June				16 June-31 June				1 July-19 July			
	Griffey		University Farm		Griffey		University Farm		Griffey		University Farm		Griffey		University Farm		Griffey		University Farm	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
0-0.33	1}		1}		0}		0}		1}		0}		0}		0}		0}		0}	
0.33-0.67	15}	35	4}	22	9}	27	3}	14	5}	20	0}	8	6}	15	2}	8	0}	4	0}	0
0.67-1.0	39}		8}		19}		3}		10}		3}		5}		0}		1}		0}	
1.0-1.33	34}		9}		13}		1}		10}		0}		6}		0}		3}		0}	
1.33-1.67	30}	50	7}	36	17}	43	3}	14	14}	43	2}	11	10}	39	1}	4	1}	43	0}	0
1.67-2.0	16}		5}		14}		2}		10}		2}		12}		0}		6}		0}	
2.0-2.33	11}		7}		6}		1}		6}		3}		5}		2}		0}		0}	
2.33-2.67	3}	11	2}	19	1}	13	4}	31	4}	14	6}	33	3}	18	6}	31	5}	21	0}	22
2.67-3.0	3}		2}		6}		8}		1}		3}		5}		0}		0}		2}	
3.0-3.33	2}		1}		6}		3}		5}		2}		2}		2}		1}		0}	
3.33-3.67	4}	4	4}	10	1}	8	1}	12	2}	11	3}	14	1}	7	2}	15	1}	8	0}	11
3.67-4.0	0}		1}		1}		1}		2}		0}		2}		0}		0}		1}	
4.0-4.33	0}		1}		2}		1}		1}		1}		3}		2}		0}		0}	
4.33-4.67	1}	1	0}	3	2}	5	4}	17	0}	3	1}	11	1}	8	2}	15	2}	13	1}	22
4.67-5.0	0}		1}		1}		2}		1}		2}		2}		0}		1}		1}	
5.0-5.33	0}		0}		3}		1}		2}		4}		1}		3}		0}		1}	
5.33-5.67	0}	0	0}	2	0}	4	1}	10	0}	4	0}	11	3}	7	1}	15	1}	0	0}	22
5.67-6.0	0}		1}		1}		2}		1}		0}		1}		0}		0}		1}	
Over 6.0	0}	0	4}	7	1}	1	1}	2	5}	6	4}	11	4}	6	3}	12	2}	8	2}	22
Totals ⁴	159	100	58	100	103	100	42	100	80	100	36	100	72	100	26	100	23	100	9	100
Median	1.26		1.65		1.53		2.78		1.71		2.97		1.97		3.44		2.43		4.80	
Mean	1.43		2.40		1.98		3.03		2.41		3.52		2.70		3.88		2.95		5.35	
SD	0.49		2.35		1.48		1.66		2.12		1.99		2.13		2.20		2.20		2.42	

¹ Heights in m were measured from the bottom of the nest to the ground beneath.

² See the Introduction.

³ Dates are those at which building began.

⁴ Half-monthly percentages were rounded and do not always total 100%.

TABLE 43
NEST HEIGHTS¹ ON TWO PARTS OF STUDY AREA²

Heights, m	Griffey Tract ²		University Farm ²		Both areas pooled	
	N	%	N	%	N	%
0-1.0	111	25.4	24	14.0	135	22.2
1.0-2.0	196	44.9	32	18.7	228	37.5
2.0-3.0	59	13.5	46	26.9	105	17.3
3.0-4.0	30	6.9	21	12.3	51	8.4
4.0-5.0	17	3.9	19	11.1	36	5.9
5.0-6.0	12	2.7	15	8.8	27	4.4
Over 6.0	12	2.7	14	8.2	26	4.3
Totals	437	100	171	100	608	100
Median	1.57		2.66		1.74	
Mean	2.02		3.17		2.29	
SD	1.67		2.17		1.89	

¹ Heights in m were measured from the bottom of the nest to the ground beneath.

² See the introduction.

predation. On the Griffey Tract the number of projecting branches and plant stems per unit of space was much greater below 2 m than above that level. Before plants became fully verdant, branches and stems provided what concealment most nests had. Therefore, it is not surprising that prior to 16 May 85% of all nests were in this shrubby stratum below 2 m and that the greatest increase in mean height occurred in the second half of May, after foliage had become luxuriant. Similarly, all of the 11 nests wedged down in tangles of interlacing twigs (type-V placement) were begun before 16 May. Other evidence that concealment played a role in the selection of nest sites is that use of evergreen plants (pines, cedars, Japanese Honeysuckle) was virtually confined to nests built prior to 1 June (p. 134; compare Bailey 1913: 302).

Variation according to section of study area.—Throughout the season nests were higher on the University Farm (median, all nests, 2.7 m) than on the Griffey Tract (median, all nests, 1.6 m); in a median test of the data pooled without regard to date, adj. Chi-square = 48.2; df = 1; $P < 0.001$. The reasons for this difference surely lay largely in the difference in vegetation of the tracts, not in the fact that they were studied in different years.

Vegetational differences in the tracts are discussed in the Introduction and reflected in analysis of characteristics of territories (Chapter 29). Griffey had smaller trees and much denser shrub cover. Since a few tall trees were present on probably all Griffey territories, the generally low placement of Griffey nests suggests a preference for nesting in shrubby vegetation when it is available. Further, Prairie Warblers tended to avoid building in the lowest quarter of the nest plant whatever its height (see below); this contributed to the greater height of University Farm nests.

Conditions from year to year.—Table 44 presents annual mean nest heights on Griffey Tract for years in which I found all or nearly all nests built. (Annual means for University Farm nests fluctuated only between 3.2 m and 3.6 m and are not shown.) A Kruskal-Wallis one-way analysis of variance reveals no evidence

TABLE 44
NEST HEIGHTS,¹ ACCORDING TO YEAR

Year ²	N	Median	Mean	SD
1957	34	1.30	1.63	1.39
1958	72	1.61	1.86	1.10
1959	58	1.27	1.54	1.02
1960	75	1.49	1.87	1.59
1961	61	1.82	2.74	2.28
1962	58	1.68	2.03	1.72
1963	38	2.06	2.95	2.64

¹ Measurements are in m. Data are from the Griffey Tract.

² Only years of season-long nest searches are analyzed.

of year-to-year differences in nest heights at Griffey ($P > 0.9$). Nevertheless, 1961 and 1963 were unusual in the large numbers of high nests in the tall trees of woods and fence rows at the edges of territories. In 1961, a frost in late May left the leaves of many shrubs and small trees withered and sparse for the season, and I was not surprised when some Prairie Warblers chose high nest sites; but I failed to notice vegetational differences, if any, to account for high nests in 1963. Precipitation was below normal, and "soil moisture became alarmingly low" in the last third of June (U.S. Department of Commerce Weather Bureau 1963: 62). Presumably scrub trees with shallow roots would have been the first to suffer from a moisture shortage, which may account for the surprising proportion (8 of 38) nests built above 4 m in height.

CHARACTERISTICS OF NEST PLANTS AND POSITIONS OF NESTS

Nest height relative to height of plant.—Table 45 presents data intended to show whether the seasonal increase in mean nest height reflected use of taller trees, or a change of nest location in trees of unvarying size, or both. Nest plants of 608 nests are segregated by height (in unit intervals of 2 m) and date (in periods of about one-half month); positions of nests are shown according to the vertical quarter of the plant in which each was placed.

The table gives the proportion of plants of each size among all plants selected per period, and it is evident that nest plants became progressively taller as the season advanced. Plants smaller than 2 m high were used less, there was little change in use of those 2–4 m high, and those taller than 4 m were increasingly chosen.

Very few nests were built in the bottom quarter of plants of any size; among the other three-quarters, the third was selected by 56.2% of the females. Seasonal variation in this respect was slight, although fewer nests (9%) were built in the top quarter of the smallest trees and shrubs at the beginning of the season than later (18–25%); this latter change was probably associated with increased concealment available in treetops after foliage reached full development. Whatever the tree's size, its lower quarter usually consisted of a leafless stem or trunk offering few forks and little concealment. In the third quarter of the majority of trees, branches and forks of the right size probably were most numerous and shelter and concealment most effective. In the top quarter of many trees the number of

TABLE 45
NEST LOCATION IN RELATION TO HEIGHT OF NEST PLANT, ACCORDING TO DATE

Date	Numbers of nests per vertical quarter ¹ of nest plants of various heights														
	Plants 0-2 m high ² Quarter of plant					Plants 2-4 m high ³ Quarter of plant					Plants over 4 m high ⁴ Quarter of plant				
	1st	2nd	3rd	4th	Total	1st	2nd	3rd	4th	Total	1st	2nd	3rd	4th	Total
April-15 May (217 nests)															
N	2	18	52	7	79	2	19	57	20	98	2	14	14	10	40
% ⁵	3	23	66	9	100	2	19	58	20	100	5	35	35	25	100
16-31 May (145 nests)															
N	0	7	27	7	41	0	10	33	11	54	0	11	22	17	50
% ⁵	0	17	66	17	100	0	19	61	20	100	0	22	44	34	100
1-15 June (116 nests)															
N	1	6	13	6	26	0	3	25	10	38	2	12	25	13	52
% ⁵	4	23	50	23	100	0	8	66	26	100	4	23	48	25	100
16-30 June (98 nests)															
N	0	4	6	3	13	0	4	24	10	38	0	7	28	12	47
% ⁵	0	31	46	23	100	0	11	63	26	100	0	15	60	26	100
July (32 nests)															
N	0	0	2	0	2	0	2	7	4	13	0	4	7	6	17
% ⁵	0	0	100	0	100	0	15	54	31	100	0	24	41	35	100
Total all periods ⁶ (608 nests)															
N	3	35	100	23	161	2	39	146	55	242	4	48	96	58	206
%	1.9	21.7	62.1	14.3	100	0.8	16.1	60.3	22.7	100	1.9	23.3	46.6	28.2	100

¹ The 1st is the lowest quarter of the plant, etc.

² For the 5 calendar periods, percentages of nest plants 0-2 m high were as follows: April-15 May, 36%; 16-31 May, 28%; 1-15 June, 22%; 16-30 June, 13%; July, 6%.

³ For the 5 calendar periods, percentages of nest plants 2-4 m high were as follows: April-15 May, 45%; 16-31 May, 37%; 1-15 June, 33%; 16-30 June, 39%; July, 41%.

⁴ For the 5 calendar periods, percentages of nest plants over 4 m high were as follows: April-15 May, 19%; 16-31 May, 35%; 1-15 June, 44%; 16-30 June, 48%; July, 53%.

⁵ Half-monthly percentages were rounded and do not always total 100%.

⁶ Pooling without regard to period, 9 of the 608 nests (1.5%) were built in the first quarter of the nest plants, 121 (19.9%) in the second quarter, 342 (56.2%) in the third quarter, and 136 (22.3%) in the fourth quarter.

TABLE 46
SPECIES OF NEST PLANTS AND FREQUENCY OF USE, ACCORDING TO DATES OF NEST CONSTRUCTION

Nest Plant	Frequency of use, by half-month											Totals	
	25 April–15 May		16 May–31 May		1 June–15 June		16 June–30 June		1 July–19 July				
	N	%	N	%	N	%	N	%	N	%	N	%	
American Elm	122	56.2	74	51.0	54	46.6	47	48.0	12	37.5	309	50.8	
Sugar Maple	25	11.5	16	11.0	10	8.6	5	5.1	1	3.1	57	9.4	
<i>Crataegus</i> and <i>Pyrus</i> spp.	20	9.2	11	7.6	6	5.2	5	5.1	1	3.1	43	7.1	
Flowering Dogwood	2	0.9	5	3.4	11	9.5	9	9.2	4	12.5	31	5.1	
Sassafras	1	0.5	1	0.7	8	6.9	3	3.1	3	9.3	16	2.6	
Blackberry sp.	6	2.8	8	5.5	5	4.3	4	4.1	0	0.0	23	3.8	
Pine, 3 spp.	8	3.7	4	2.8	0	0.0	1	1.0	0	0.0	13	2.1	
Red Cedar	7	3.2	2	1.4	0	0.0	0	0.0	0	0.0	9	1.5	
Others ¹	26	12.0	24	16.6	22	19.0	24	24.5	11	34.4	107	17.6	
Totals	217		145		116		98		32		608		

¹ These plants, with the number of nests built in them, were Black Walnut, 16; American Hackberry, 11; Black Locust, 9; Redbud, 9; Black Cherry, 7; Honey Locust, 7; apple, 7; ash sp., 5; Red Maple, 4; Sycamore, 3; Shining Sumac, 3; Chinquapin Oak, 2; Red Mulberry, 2; Hop-Hornbeam, 2; Tulip Tree, 2; Wahoo, 2; Slippery Elm, 2; Black Gum, 2; Shagbark Hickory, 2; Smooth Sumac, 2; Osage Orange, 1; plum sp., 1; Box-Elder, 1; Roughleaf Dogwood, 1; Coralberry, 1; Ohio Buckeye, 1; American Linden, 1; Silver Maple, 1.

suitably rigid branches was smaller and exposure to sun usually greater (see below).

Orientation and exposure.—I attempted to determine whether 592 nests tended to be oriented toward any particular compass quarter relative to the vertical axis formed by the trunk of the nest plant. No such tendency was detected.

In a rough classification of degree of exposure to the sun, 68 of 482 nests (14%) received direct sunlight much of the day; 31 (6%) were directly exposed no more than 1–2 hours, excluding time when rays hit the outer walls rather than the cavity; 251 (52%) were never in direct sunlight but for at least several hours were exposed to flickering sunlight through foliage; 132 (28%) probably were never touched by direct rays or were touched only momentarily. Very few nests were in deep shade.

Species of plant.—Approximately 750 nests were built in about 40 species of trees and shrubs. All but the rarest trees were used at least once. In addition, the vines of grape, Virginia Creeper, Japanese Honeysuckle, and Bittersweet were used.

Table 46 distributes 608 nests according to plant species in which built, by approximate half-month intervals. American Elm, with 51% of the cases, was by far the most important nest plant. Of the others, only Sugar Maple, hawthorn spp., and Flowering Dogwood were selected more than 5% of the time; and even the most frequently used of these contributed only 9% of the total.

Among the many nest plants of Prairie Warblers reported in the literature a few not among those listed in Table 46 are mangroves (A. H. Howell 1932: 409); scrub oaks (Daniel 1901; Sutton 1967: 511); hickory (Coues 1888); Barberry (Brewster 1906: 346–347); birch and Bayberry (Sage *et al.* 1913: 159); Sweet Gum (Pearson *et al.* 1919: 298); Creeping Juniper (on Ontario beaches; James L. Baillie, Jon Barlow pers. comm.); see also Walkinshaw (1959).

Preferred and avoided nest plants.—Comparison of frequencies of trees on the study area and frequency of selection of these for nest sites indicates the Prairie Warbler's preferences. I attempted to count every tree at least 1 m high in three typical disjunct fields totaling 9 ha in area. Counts need not be presented, but certain percentages are of interest: American Elms made up about 25% of all trees, Sassafras 24%, Redbud 19%, sumac spp. 9%. Obviously the warblers selected American Elms out of proportion to their numbers; their many crooked branches and twigs and the frequent forking and reforking of their upright branches offered nest placements of the two most favored types. No other species appears to have been distinctly preferred. Sugar Maple and Flowering Dogwood were selected approximately in proportion to their numbers.

Trees used much less than expected if selection were random were Redbud (few small lateral branches and few upright forks), sumac spp. (in form much like Redbud), ash spp. (saplings have symmetrically opposed pairs of lateral branches with a few upright forks; compound leaf form offers little concealment), Black Cherry (small branches are probably too devoid of Y-forks, too lacking in multiple twiggy formations, and possibly too flexible), and Sassafras (young trees have a simple, symmetrical pattern of branching and lack upright forks and leaves growing near the trunk).

Shapes and sizes of most species' leaves probably were of little importance in selection of nest sites, but the distribution of leaves and twigs on branches appeared

to be very important. For example, a major difference between small elms and small Tulip Trees, which were avoided, is the tendency for twigs and leaves to grow along the full length of smaller elm branches but toward the ends of Tulip Tree branches, away from the trunk.

That several species of trees tended to be selected during only part of the season is evident. Only 1 of 22 nests in pines and cedars was begun later than May; apparently these trees were avoided except when deciduous trees were still rather bare. Japanese Honeysuckle was used only in April and May, presumably for the same reason. Sassafras was for the most part avoided until after 1 June; larger sassafrasses lacked the unsuitable branching characteristics of young specimens and were acceptable when nests were placed in bigger trees later in the season. The concealing effect of twigs and thorns of hawthorns and crabapples has already been suggested as a reason for the more frequent use of these at early dates.

LOCATIONS OF NEST PLANTS

Location relative to territory boundaries.—In five seasons I measured distances separating 138 nests from the nearest boundary. Boundaries were sometimes vague zones between neighbors (Chapter 29), and numbers are approximate. Boundaries separating adjoining territories are referred to as "interior," others as "exterior." A nest more than 40 m from the nearest boundary is classed as being "in midterritory."

Thirty-eight nests were in midterritory, 36 nests 40–20 m from a boundary, 26 nests 20–11 m, and 38 nests 10–0 m.

Of the 100 nests within 40 m of a boundary, 29 were within that distance of an interior line, but 19 of these were near rarely contested zones constituting a sort of no-man's land. Thus a mere 10 among 138 nests provide clear-cut cases of location within 40 m of a line at which neighboring males met. The shortest distance between a nest and an interior line was 15 m (two cases). The ratio of length of exterior to interior lines on the territories involved I estimate from sketch maps as roughly 1:1.5–2. The many approximations do not justify statistical analysis, but the data point to two conclusions: (1) The middle of the territory was not preferred; rather, exterior lines may have been preferred. (2) Nests within 40 m of boundaries were more often near exterior lines (71 cases) than would be expected by chance and were rarely (10 cases) near boundaries that males defended vigorously (compare Mayfield 1960: 48). This subject is discussed further on page 135.

Exterior lines usually coincided with the margin of Prairie Warbler habitat. When this margin was woods females often selected a tree at its edge and occasionally even entered the woods as much as 20 m to build. When the boundary was the junction of shrubland and mowed field, females necessarily stayed within the territory to nest but showed no tendency to maintain a zone of suitable habitat around the nest. Four nests overhung mowed fields.

Several females selected sites in typical habitat but beyond an exterior boundary of the territory, causing the male to take possession of the area (see Chapter 29).

Distance between nests of females on different territories.—It follows from the

foregoing that nests in use simultaneously on different territories were rarely less than 80 m apart. The closest separation was 50 m, but the mate of the female that built first had disappeared by the time the other female began to build; therefore placing the second nest near the first did not involve close approach to a currently defended interior line. The closest nests on adjoining territories both occupied by males were 55, 65, 65, 80, and 95 m apart.

The mechanism responsible for the apparent avoidance of interior boundaries, and therefore for the distance between simultaneously active nests, may have been the females' shunning of the scenes of male fighting. The interest of males in nest building on neighboring territories and the resulting quarrels are described in Chapters 7 and 30. The disadvantage to females of being subjected to a neighbor's intrusions seems obvious, and selection of sites near exterior lines probably reduced intrusions. A frequently proposed function of territory is reduction of interference with reproduction (e.g. Hinde 1956: 357; see Chapter 29); choice of a nest location that would minimize interference is congruous with that function.

Distance between nests of mates of polygynous males.—Approximate distances between simultaneously active nests of mates of polygynous males were measured in 36 cases (excluding cases of males holding two disjunct territories; see Chapter 29). The minimum was 50 m, the maximum 300 m, the mean 124 m (SD 59 m). Only twice did a female build within 60 m of a nest of her mate's other female.

A mean separation of 124 m is large, considering sizes and shapes of territories (see Chapter 29). The suggestion is that females tended to avoid each other in locating nests. Females with the same mate sometimes watched each other closely and once fought strenuously (p. 369); very likely each always knew the location of the other's nest on the territory.

Distance between nests of Prairie Warblers and of other species.—The two cases of least separation involved Field Sparrows. A warbler nest was 2.5 m from a sparrow nest that had been built about the same time. Another was 8 m from a sparrow nest that was completed probably on the day before the warbler began building. Walkinshaw (1959) found an Indigo Bunting nest 9 m from a Prairie Warbler nest.

Nest location relative to nearby trees.—In 577 cases, I classified locations of nests with regard to numbers and positions of nearby trees. The categories were rough and will not be described in detail; the results show no narrow preferences in this respect. About 27% of the nest trees were at least 5 m from other trees; 17% were in the center of small open clumps of trees; 17% were in the center of small dense clumps; 37% were at the edge of large dense clumps of trees or mature woods (and were randomly distributed with respect to north, south, east, and west edge); and 2% were in woods. Proximity of other trees appears of little or no importance, except that mature woods were usually avoided.

When nests were built within dense clumps, such clumps tended to be composed of trees of about equal size. A few branches projected above the general level of the top of the clump; below the top, leaves and branches were thickly interlaced. Almost invariably in this situation nests were placed in the projecting higher branches, 0.1–1.0 m above the top of the clump and therefore in a position analogous to that of a nest in a low tree standing among forbs and grasses.

DISTANCES BETWEEN SUCCESSIVE NESTS OF INDIVIDUALS

I measured distances between 193 unsuccessful nests and their replacements and between 22 successful nests and the females' second-brood nests. Nests of females that changed mates and territories were not considered.

The five minimum distances between predecessor nests and their replacements were 10, 12, 13, 14, and 19 m; the five maximum distances were ca. 285, 270, 253, 250, and 250 m. The mean of the 193 cases was 85 m (SD 53 m). Observed distances were compared with calculated expected distances under the hypothesis that replacement sites were randomly selected with respect to distance. The hypothesis cannot be rejected; no pattern, e.g. avoidance of the vicinity of a nest that failed, is indicated. Similarly, no tendency is evident to locate a replacement nest at a greater or lesser distance from its predecessor according to whether the replacement was the second, third, etc., in the female's series of nests that season.

The minimum distance between a successful nest and a second-brood attempt was 34 m, the maximum 200 m, and the mean of 22 cases was 81 m (SD 47 m). This mean does not differ significantly from that separating unsuccessful nests and their replacements. The vicinity of the successful nest was apparently neither preferred nor avoided.

RE-USE OF NEST SITES AND NESTS

Multiple use of sites.—Despite almost unlimited numbers of suitable nest sites on every territory, at least 12 trees were selected more than once, and 4 were used 3 times each. Within the group of 12 trees, 10 nests were placed in the exact site of an earlier nest. Six sites were used twice (compare Brooks 1932) and two 3 times; thus 8 sites held more than 1 nest during the study. In 4 of the cases of double use, the nests were built in successive years; once 1 year was skipped; once 2 years were skipped. One case of triple use was spread over a total of 4 years, one over 5 years.

No re-use was by the female that had built the earlier nest. In only three cases was the male on the territory the same bird in both years a site was used. Thus the cases cannot be explained as the result of individuals' remembering nest sites of earlier years. I detected no reason why the re-used sites might be especially attractive. Reproductive success was no greater there; in all of 14 cases for which the information is known, the later nests failed.

Possible re-use of nest.—One nest may have been used by two females. A predator took the eggs in it on 7 June, disturbing the lining and padding slightly. The female renested, failed again on 24 June, and disappeared. The male acquired a new female, which began a nest on 28 June. I intentionally disrupted building, because the nest was too high for a proposed experiment and I hoped she would begin again at a lower elevation. For the next 5 days during many hours of observation the female was not seen to build. Instead the pair stayed together, behaving as during laying and before incubation; they showed some alarm near the site of the nest first mentioned, above. On 5 July, I happened to brush by the site of that nest, and the female flushed from the old nest or one placed in the same spot. It contained three eggs, which hatched on 15–16 July; assuming an

incubation period of the usual length for that date (Chapter 23), egg 1 had been laid no later than 2 July.

The evidence that the second female laid her eggs in another bird's nest is as follows: (1) If the nest had been newly built, I would probably have observed the building, considering my concentrated search in the very part of the territory where it was located. (2) The behavior of the pair prior to 5 July was quite different from normal behavior during building but was typical of that after building and before incubation. (3) Laying of egg 1 on 2 July, inferred from the date of hatching, would have been expected of a female that began to build on 28 June, as this female did; the timing of events is inconsistent with the hypothesis that she built the nest in which she laid. (4) The experiment (pp. 158–159) in which a female accepted and laid in a complete nest supplied by me and terminated building prematurely proves that it is possible for some individuals to omit a large part of normal building behavior and to lay in another female's nest.

CHAPTER 16

BEHAVIOR DURING BUILDING OF NESTS

BUILDING THE OUTER SHELL

Early movements.—The earliest material placed in the nest site was webs, which were put in position as the female sat or stood where the nest was to be. Webs were stuck to branch and leaf surfaces by many rapid, craning head movements; the bill thrust forward, sideward, and backward toward the base of the tail. During the average period at the nest (about 30 sec) the female usually interrupted her quick, shuttle-like head motions once or twice and pivoted. Sometimes she rose and thrust webs beneath her body, but most were placed where exterior walls were to be built. If the female built a basal wad (p. 122), she entered the site and placed bast and webs beneath her while standing, then poked the material into position with downward stabbing motions, compressing it by sitting on it and kicking. Rotation of the body was frequent; shaping movements of breast and belly (described below) were also used.

Forming cup.—Disregarding the basal wad, if any, most females began nests by making a shallow saucer-shaped foundation of fibers and subsequently building up a thick outer shell, so that the wall rose gradually. Much less commonly, females first built a very thin full-size shell, then added materials to the inside to thicken the wall. Thickening began at various points; some even thickened the rim first, producing a rudimentary cup hanging below a well-made rim (compare Stanwood 1910a).

Females that constructed a thin cup before thickening it built as follows: They carried the outermost fibers into the site; thrust the head beneath the belly and laid strands across the site, sat on and bent these into a concave shape, seized loose ends projecting outward and upward, and fastened these to the prepared web-covered surfaces. Fibers for vertical walls were placed nearly horizontal in front of or beside the builder as she sat in the nest; sideward head movements stretched loose ends around the rim of the prospective cup until they were attached at two or more points; strands seemed to be threaded through the slightly opened bill. As the cup formed, stabbing bill movements were introduced and probably inserted sections of fiber into the developing nest. Webs were added at least as often as plant substances and strung from supporting branches to the nest and from point to point on the nest. Thickening the bottom and walls of the skeletal shell probably involved most behaviors to be described in the next two paragraphs.

Females that built a solid bottom, then solid walls from bottom to top, behaved as follows: They carried fibers into the nest, laid them across the site, and pressed them into shape with the belly and breast. While sitting on the materials, they often craned the neck outward and downward, seized a loose end and drew it inward and toward one side, then fastened it to the supporting plant or to the nest foundation. This resulted in formation of a compact, slightly concave disk

(nest floor). When the disk was thickened to satisfaction the female added fibers on top of its periphery, carrying them into the site and placing them horizontally either in front of her or to one side, turning her head as much as 100° from the long axis of the body. Usually she remained in the nest and started to incorporate newly brought fibers, pivoting the body and constantly pulling projecting loose ends both inward and sideward in the direction toward which she turned. Thus new material laid around the periphery (the developing walls) was bound down by fibers drawn inward and over that material and then stabbed into position inside the nest. A lateral texture resulted. Webs were brought every few trips and fastened either to supporting branches or to the nest exterior. After leaning out to attach them, at times far down toward the underside of the nest, the female pulled webs inward over the wall, binding down the plant material with bill jabs (up to 10 jabs around a 60° arc); the fastening process lasted about 10 sec.

As the wall began to rise, the female introduced a movement. After pushing newly brought fibers downward onto the wall's top, she raised her head and stabbed vertically several times, apparently both packing the material and inserting sections of it into the wall. Material was probably always laid toward the inside edge of the wall's top; all head and body movements (see below) pressed it downward or stretched it outward, or both, tightening the shell and making the wall compact.

Movements of limbs and body.—After the nest consisted of a small mass of fibers, females following either construction sequence (above) usually used limb and body movements; they began these 5–10 sec after putting newly brought items in place with bill and head movements. Head movements often continued simultaneously with the following body movements.

Wing shaping: Just as during site selection (see p. 103) the wings at times were extended slightly at the wrists as the female turned; occasionally they stretched nearly full length when there was no resistance from a branch or leaf. The movement possibly was functionless at the very beginning of building but may have provided information about the site. As the nest developed, the wrists pressed downward and outward against the interior walls; the primaries spread slightly, and pressure on the wrist at times caused the tips of the outer primaries to be elevated and to cross over the back. Shaping with the breast and kicking (below) probably always accompanied wing shaping.

Kicking: Early in building, the feet sometimes thrust downward and backward out of the site, as during site selection. After the shell developed, the female kicked the feet rapidly and alternately, both at the bottom of the nest and the wall behind her. Often kicking was manifested only by the jerking of her body, but her heels were visible when she leaned forward and kicked at the rear wall. In this position the breast pressed and probably shaped the wall in front of her, and she usually rotated.

Throat and tail shaping: Sometimes the female stood and pressed her throat down on top of the wall. In an important tail-shaping movement, the region of the crissum pushed downward against the partly erected nest wall, usually while the female kicked the bottom of the nest. Tail shaping and throat shaping were associated at times. The female sometimes pivoted, smoothing the top of the

incomplete wall with throat and tail. Occasionally when the wall was still very low, her rectrices were depressed and projected downward.

Thickening outer shell.—Probably all females thickened the shell with stiff short plant fibers, inserting these while perched outside the nest on its rim or on a branch; these were the first insertions made while outside the nest. Females then entered, sometimes immediately packing the new material by the body and limb movements described, at other times arranging it with the bill before sitting and shaping. Any loose fiber ends outside the nest were pulled laterally inward over the rim and fastened.

BUILDING THE PADDING AND LINING

Soft, usually short substances were inserted while the female perched outside. Rarely she left without entering. When she entered, she did so immediately and performed some or all the shaping movements described above, ordinarily turning several times. She used the bill infrequently, occasionally pecking beneath or beside her at the bottom of the nest.

Fibers of the lining were placed and shaped by the movements performed in padding. Use of the bill was rare.

GATHERING BEHAVIOR

Radius and direction of gathering.—Because of various problems of observation, distances recorded are probably biased in favor of unusually short and unusually long carrying trips. Distances (which are approximate) were affected by the stage and day of construction, which also had considerable influence on the materials used (Chapter 15) and some influence on the rate of building (Chapter 17).

About 75% of the material in the outer shell was collected within 25–30 m of the nest (some 300 observations), about 5–10% within 3–10 m. Carrying beyond 25–30 m was probably largely confined to situations in which the female had been foraging, then began to search for material wherever she happened to be when ready to resume building. The longest observed trip to build the outer shell was 60 m. If a nest was not near a source of bast fibers, the builder went to suitable plants at the necessary distance.

Possibly because padding material was usually less varied (more specialized) than outer-shell, I sometimes saw it carried as far as 110 m; but probably 60% of all (300–400) trips were from within 30 m of the nest (compare Walkinshaw 1959).

The shortest observed trip with lining was 40 m, the longest 150 m, the mean (of about 200 cases) 80 m. This increase in carrying distance probably was caused by the slow rate of building at this stage (Chapter 17) and the tendency of the female to move considerable distances from the nest between her infrequent trips.

Compass bearings of individual's flights from the nest to gather material rarely suggested random distribution, probably because of the nonuniform distribution of suitable materials and the persistent exploitation of discovered sources.

Height and manner of gathering.—Probably 90% of all nest material was col-

lected on or within 0.3 m of the ground. A common exception was fiber from grape vines, gathered at heights of 3–16 m. Osage Orange bark fibers sometimes were pulled from high limbs; tent caterpillar webs were collected at heights up to 6 m; spider webs were taken wherever found, including treetops.

Webs usually were taken in the bill and detached by retracting the neck and head. Spider webs were often seized while the female hovered in mid air; loud bill snaps were audible at times. Soft fibers were pulled off while the female perched, usually on the plant itself. She took the end of a fiber in her bill and backed away, tugging as she went; if the plant was upright, she backed down it. When fibers offered resistance, she jerked her head backward and slightly side-ward, retreating a few cm at a time until the connection with the stem broke. Stiff fibers could not be peeled off in this way and were broken by jerks of the head and neck. Wiry grasses were gathered while the female stood on the ground; some were broken at the base by jerks of the head. At times she backed away as far as possible until grass was taut; occasionally dead grass was uprooted. Plant down, especially fruits of Broomsedge, was often gathered while the female hovered, but sometimes she alighted on the stem.

Flight to nest.—Directness of routes to nests varied. Most birds ignored me unless I was very near the nest, passing right by me on a straight-line flight to the nest, landing within 1 m of it and going to it immediately. Some builders took circuitous paths, flying around me and approaching the nest from the side opposite me; rare females appeared to skulk to the nest through low cover.

Two kinds of behavior may have been cryptic: (1) Some females building in the edge of woods consistently entered or left the woods at a point to one side of the nest, then when screened by the foliage turned and went to it. (2) At times females building close to the ground gathered material near me, flew to the largest tree nearby and ascended to its top, headed toward the nest in high flight and landed in a treetop near it, then descended quickly to the nest. Both forms of behavior made it difficult to fix the nest's angle and to judge the height at which to search, but this result may have been accidental. Blue Jays and/or cowbirds may exert selection pressure for such cryptic building behavior, but it is questionable that it would then be given in response to a human.

Females with material usually flew with a characteristic steady beat, the wings probably not as fully folded against the body between beats as they are in unencumbered flight. The wing stroke seemed shallower and air speed slightly slower than normal. The weight of the material or its screening of forward vision may have been responsible.

Flight from nest.—Females nearly always flew directly and fast to gather more material, leaving higher nests with a steep swoop to just above the ground cover. Some females varied their behavior, swooping down at times, at others flying directly from the nest at its height, at still others descending or ascending within the nest tree and then leaving.

MISCELLANEOUS FEMALE BEHAVIOR

Embedding of cowbird eggs.—Among many instances of cowbird parasitism of Prairie Warblers (Chapter 32), I saw only two or possibly three cases of

partial embedding of eggs. At least two cowbird eggs and probably the third were laid while the warbler nests were being built (compare Mayfield 1960: 156). One egg was 66% buried; two were half buried, but one of these may have settled in a depression in the cavity instead of having been embedded. The cases may represent the kind of behavior from which has evolved the familiar defense of the Yellow Warbler against the cowbird (Bent 1953: 174). Bailey (1925: 129), in fact, stated that Prairie Warblers often build a false bottom over the eggs of the cowbird and host eggs already present; and Sprunt (Griscom and Sprunt 1957: 183) reported but has never himself seen (pers. comm.) an instance of this behavior.

Dismantling of old nests.—Six females dismantled old nests or fragments (six built by Prairie Warblers and two by American Goldfinches) and incorporated the material into new nests or fragments. Two engaged in the behavior while building more than one nest, so there were eight cases. In addition, several females were seen carrying very large loads of material that looked like parts of old nests. Extreme dates of dismantling were 5 May and 5 July. Five dismantled nests had been built by the dismantling female herself, but two individuals contributed two of these instances. One had ceased to use her former nests 15 days and 37 days before dismantling them, the other 19 days and 1 day. In cases in which females stripped nests not their own, two took material from goldfinch nests of the preceding year; the other joined a male in midseason and used the nest of her predecessor as a source for her own nest.

In all but 2 instances, I saw only 2 or 3 loads of material pulled from the old nest, which was not demolished. One female, however, built a thick outer shell on 13–14 June, then began a new nest 20 m away at 1200 on 14 June. She repeatedly took material from the abandoned shell, which by 15 June had disappeared. The second female removed all signs of a fragment that had taken her some 3 hours to build. (See also Wilson 1922, Gray 1924, Morse 1925, and Sturm 1945.)

Building after beginning of egg-laying.—As described (Chapter 17), females carried and incorporated material on their occasional visits to the nest between the end of active building and the laying of egg 1. After laying began and increasingly often as the clutch neared completion, they sometimes visited and sat on the nest for short periods (see Chapter 21). On two such visits, one on the day egg 1 had been laid and one on the day egg 2, females carried grassy lining material to the nest. One dropped her load upon seeing me; the other took the grass to the nest and placed it on the rim.

REACTIONS OF FEMALES TO INTRUDERS

Reactions to birds.—Nine building females reacted to birds of other species in or near the nest tree. Two intruders were Blue Jays. In one of these cases the warbler began to Sputter and immediately thereafter the jay flew to the nest, thrust its head into the cavity, and sat at the nest 10 sec; the warbler hopped and flew around nearby, calling many Tsips and a few Cheks. The jay left and the warbler then directed her alarm toward me; until then she had shown no awareness of me. The nest, in the early stage of being padded, was deserted.

A Nashville Warbler (4 m from the nest), an Eastern Wood Pewee (2 m), and two Field Sparrows (each 2 m) were attacked by female warblers that flew directly at them and forced retreat. When a male Rufous-sided Towhee landed in a nest tree 2–3 m from the nest, the warbler immediately arrived and perched, her tail bobbing nervously, 2 m from the nest and 3 m from the towhee; it left in 30 sec, and the warbler waited 30 sec before flying away. A female warbler foraging near her nest stopped when two male cowbirds began to display 15 m from her; she sat quietly watching them until they flew away 1 min later.

Reactions to humans.—Reactions to humans varied. Many females sat watchfully in their nests if I approached while they were building and flew when I was 1–8 m away. Some flights resembled low-intensity moth flight of males (Chapter 7) and suggested incipient distraction display (Chapter 25). Full-intensity distraction displays were observed only 6 times during building, never on the day building began; 4 females were in nests and fluttered out when I was 1–4 m distant; and 2 approached me at the nest and displayed. In behavior observed once at this stage and occasionally during incubation, a female about 15 cm from her nest quickly got into it and sat quietly when I approached. Nine females gaped at me briefly (maximum 15 sec) but with no accompanying displays. Two that were gathering material faced me and gaped; 5 at the nest left it (3 toward me, 2 away from me), then gaped; 2 flew toward the nest as though guarding it and gaped when I approached.

Other reactions to my presence were dropping nest material, refusing to go to the nest, uttering alarm calls, and retreating. Usually building did not resume for at least 10 min, but females showed much individuality. One that I had never approached or disturbed in any way was reluctant to go to the nest when I watched from 100 m away. In contrast, a female let me place a hoop net around her nest, then built while I sat 4 m away; even after I tried and failed to chase her into the net, she built when I stood only 20 m away.

In experiments to test females' tolerance of me at this stage, three birds working on outer shells of first nests (second day of building) abandoned them after I had sat 8 m away for some 30 min. Later in the season other females continued to build in these circumstances (see Heinroth and Heinroth 1959: 39).

The reaction of a female that I disturbed in order to cause her to build in a different site was as follows: I threw balls of mud at her each time she approached a high nest on the second day of building, the balls showering fragments of mud around her. On her first effort to go to the nest I had to throw six times before she gave up; after each throw she retreated a little and made another approach. She disappeared for 15 min, then returned and tried again; I drove her away with two throws. This was exactly repeated 15 min later, after which she abandoned the nest.

Reactions to mounted specimens of birds.—Building females usually showed no more aggressiveness toward strange males than toward their own mates, but one reacted aggressively to a mounted male Prairie Warbler placed 11 m from the nest. After inserting nest material she flew to within 1 m of the mount, gaped motionlessly for 20 sec, then gradually approached to within 10 cm. During the entire time (1 min) her bill was open; part of the time she performed wings out (pp. 43–44). She seemed intent but not fearful. Finally she turned and flew away.

Four times on the second day of building I placed a mounted female cowbird 1–2 m from nests while the builder was out of sight. Two cases will illustrate reactions: In the first, the female arriving with material apparently saw the mount when 5 m from it and flew straight at it but veered off when 1 m away. She then flew and hopped about nervously, bobbing her tail and once depressing it slightly and fanning it, flirting her wings; she did not approach the nest more closely than 8–10 m (in 6 min). The nest was completed. A second female flew toward her nest tree, saw the mount, immediately continued her flight past the nest and out of sight. Nothing more happened (in 7 min) except that the male came up, hopped about nervously, then left. This nest was abandoned.

These experiments, though crude, suggest that female Prairie Warblers will not make building trips if a female cowbird is near the nest. The warbler that left the vicinity of the nest when she saw the cowbird may have been giving a cryptic response of possible value if the cowbird has not yet found the nest. Some builders may desert the nest if they see a female cowbird near it.

BUILDING FEMALE'S BEHAVIOR TOWARD MATE AND FIRST BROOD

Copulatory behavior and its frequency during nest building have been discussed above (Chapter 12), as have displays and other sexual behavior that began during pair formation (Chapter 10). For convenience, the interactions of the pair that have special pertinence to the nest building period will be presented in connection with the discussion of the male's behavior, in the next section.

Four of seven females whose second-brood nests I discovered during building tended first-brood fledglings while the new nests were under construction. Selected details are described on page 167. Three carefully observed individuals were never seen to tend young after they started to build. As further evidence that some females probably become unresponsive to fledglings at this point, the bird that deserted her brood within a few hours after their nest-leaving and paired with the male on the adjacent territory (case 3, p. 347) altogether disregarded her fledglings, although they were often within earshot and sight.

MALE BEHAVIOR

Male behavior tended to fall into three phases during nest building: (1) the first few hours, when there was evidence of high stimulation, including some entering of the nest; (2) most of the rest of active building (see definitions, Chapter 17), when the male spent much time near the nest watching building; and (3) the final day of active building and all of inactive building (see definition, Chapter 17), when he usually accompanied the female. Details are given below.

Entering nest.—Throughout the active phase the male visited the nest and nest tree; most such visits apparently were caused by attention to the female and the tendency to watch or follow her (see below) rather than by attraction to the nest itself. However, certain males showed great interest in the nest and entered it (see Mousley 1926, 1928; Harding 1931; Graber and Graber 1951; Bent 1953: 166; Lawrence 1953b), sometimes performing behavior that may have been pseudofemale and caused by highly aroused, unfulfilled sexual motivation (see the discussion, p. 109).

Thirteen of 15 observations of males (seven individuals) that sat in the nest took place during the first 4–5 hours of building; dates were 9 May–5 July. Two males went through nest shaping motions (see above), one sitting in the nest for 5 min and manipulating fibers in the manner of a female; during 1 min the female came to the nest rim and also worked with the material. Another male sat quietly in the nest for 3 min. Usually the females were not at the nest when the males went to it; three times males stayed until females arrived with material. The behavior of a pair when together at the nest will be described in the next paragraph. Once a male went to an abandoned fragment and sat in it 1 min; his mate probably had not yet begun her new nest. And on the fourth day of building of a nest with a 7-day active phase, I found the male sitting in it.

This paragraph reports events at a single nest on 12–13 May. The male's reactions were unusually intense. The female built three fragments (12–13 May). On 12 May the male sat in a fragment and sang his preferred group-A version, then got out and sang beside the fragment; the female was not present. At 1615 on 13 May, the male went to the nest (begun at 1500) and entered. The female appeared with material and tried to get in; the birds were in contact; the male opened his wings (wings out or wing waving?) at the female, which gaped; the male retreated a few cm and left. At 1627, the female was in the nest when the male came and got in beside her. She gaped and while holding her bill open pecked three times at his nape; he left after 15 sec. At 1659, the male had been singing and watching the female's frequent building trips. He went to the nest and stood outside it until she arrived; he then got in and sat. She waited 3 sec until he had left, then entered and built. At 1747 the male and female arrived together. He entered first, and she crowded in beside him; they sat side by side for 4 sec, peacefully except for slight jostling. The male left in butterfly flight. At 1752, this performance was repeated, but this time the female pecked at the male for 3 sec before he departed in butterfly flight. (I quit watching at 1755.) During several hours of observation next day between 0620 and 1630, the male did not enter the nest but behaved excitedly in the usual ways described below.

Watching female.—In some 95% of about 500 cases, prior to the final day of active building males spent most of their time watching their mates during periods in which they were making frequent building trips. Males perched usually no more than 30–40 m from the nest, which corresponds to the radius within which females usually gathered outer-shell and padding material (p. 140). A male whose 60 consecutive perching locations I recorded was within 20 m of the nest tree on 60% of them, within 30 m on 75%, within 40 m on 90%; all perches were within 50 m. (The territory was large; perches were available on it at distances up to 150 m). Most observing by males was from the highest trees around the nest, ordinarily either from the top or the ends of high branches affording the best view. All males seemed to develop preferences for certain trees, especially dead leafless ones; some chose 1 or 2 trees, but 4 to 6 were used if available. If the nest's location permitted, observation posts were distributed roughly circularly around the nest. Trees shorter than 3–4 m were rarely used.

Males usually moved nearly continuously from one tree to another, rarely staying on a perch longer than 30 sec. They often flew to a perch overlooking the area where the female was gathering; therefore by watching the direction in

which a male looked, I could locate the female and follow her to the nest. In contrast to this moving about, sometimes males sat motionlessly while staring fixedly for long periods (maximum 7 min).

If only one high tree was near the nest, the male sat in it and flew little; if no high tree was nearby, he retreated as far as necessary (up to 100 m distance) to find one. When the perch was far from the nest, he occasionally flew out toward the nest and back, sometimes hesitating slightly in the air when above the nest.

A few males appeared to pay no attention to building after the first day. There were probably individual differences; three males behaved in this unusual way in two different seasons.

Male pounces and chases.—I observed 61 male swoops on nest-building females. Twenty females flew and sexual chasing ensued (14% of 192 observed sexual chases were during building). Eleven times females did not fly and responded aggressively; one female whose mate alit in the nest tree flew at him and drove him away, and another flew at the male in a flutter-up (pp. 49–50). Thirty females simply showed indifference; if perching when the male approached, they paid no apparent attention; if flying, they immediately perched and sat quietly until the male went away.

Many pounces (30 of 39 recorded cases) began when females started to fly toward the nest with building material. The 61 cases of pouncing were randomly distributed during the season and hours of the day. Of those that can be assigned to a stage of building, 24 fell on the day building began, 26 on remaining days before the final day of the active phase, and 4 on the final day (none during the inactive phase).

Accompanying female.—At all stages of reproduction the male sometimes followed and watched the female as she foraged, also foraging himself. This quiet associating was most frequent when overt reproductive behavior (e.g. building the nest, incubating, tending fledglings) was at a minimum. Thus, on the final day of building and also during the inactive phase the pair often foraged together.

Accompanying the female during her building trips also occurred, on all days of the active phase and inactive phase but much less often when the rate of trips was fast. On the final active day when she made fewer trips, virtually every male accompanied the female on a large share of these. In a typical case, beginning with the female's fourth trip of the day at 0637 I saw the male return with her 13 times on her next 28 building trips. It is likely that this increase in accompanying on the final day was associated with the increase in the female's gathering radius (p. 140), which usually made it impossible for the male to observe her from posts near the nest. If his interest in her during nest building functioned to protect her against surprise attacks by predators and insemination by other males while she gathered nest material, as seems likely, it follows that when building trips became fewer and gathering distances longer it would be more advantageous to accompany her than to wait for her at the nest. This would also be the case during inactive building. Occasionally females became aggressive and drove away mates that approached too closely (1–2 m).

A typical observation of accompanying behavior follows: The female gathered fur at the entrance to a fox den, 100 m from the nest; the male perched 3 m above and watched intently, his head bent far down and his tail drooped as a counterbalance. He did not flirt his wings excitedly or pirouette while he watched, although many males did this. He sang 13 very faint songs (group-B) in 6 min. The female then flew up to perch with the material, and he joined her. They started toward the nest; the male outstripped the female and landed 1 m from it just before she arrived. During most of her 2 min in the nest he hopped about within 1 m of her, singing 1–2 loud Trills. When she emerged and flew straight away, he followed close behind.

Singing.—Songs were frequent until the final day of active building when the male began to accompany the female (see Tables 11 and 12). Cadence was unusually irregular, and in some 30% of about 300 instances volume was less than full. The arrival of the female at the nest on a building trip frequently caused a change in the male's singing, usually a reduction in volume but occasionally an increase. Most males sang less while females were at the nest.

Guarding nest.—Some males attacked other birds near the nest, but males rarely showed concern comparable to that of females. Thus, although one male chased Field Sparrows from the nest three times in one afternoon, more typical was a male that watched a female American Goldfinch dismantle the nest his mate was building; he merely called Chek and went to the nest after the goldfinch had left. In only five among hundreds of occasions on which males must have seen me at their incomplete nests was there any discernible reaction (one or more of the following: approach, Tsip calls, group-B song, silent and tense watching). But one male flew in undulating flight nearly straight upward, hovering over me 3–5 sec, behavior that was commoner near nests containing young.

Behavior of polygynous males.—I considered whether male behavior during building was affected by the presence of another female and family. Males having one female exploring for a nest site when the other was padding a nest stayed with the former and engaged in normal pre-nest-building behavior. When both females were building simultaneously and were at the same stage of construction, males (three cases, all stages of active building) were equally attentive but by turns. Intervals between alternations of attention were less than 30 min, often much less.

Four males had one female that was just beginning a nest while the other was at a later stage of building. Three of these were observed paying attention (typical behavior) only to the female that had just started to build; the other divided his attentions. This possible tendency to watch the beginning of building may be additional evidence that males were especially stimulated by that stage. A male with one female (female A) lining her nest and another (female B) padding hers was mist-netted beside the nest of female A. On the day before, when female B had begun to build, he had been almost exclusively interested in her and had been netted at her nest.

A male with one female in the active and another in the inactive phase of building stayed near the nest under active construction, behaving normally for that stage. A male apparently paid no attention to a female that had begun to lay eggs and concentrated on a second mate that was building. Males (nine cases)

ignored incubating females in favor of building mates; these they watched and accompanied, behaving appropriately for the stage of building.

A male that had 7-day-old nestlings by one mate and another female in the second day of building divided his attention between the nests. From 1420 to 1522, I watched the building female. The male was with her at 1422–1447, 1458–1512; during the rest of the hour he sang, apparently near the nest with young. From 1700 to 1800 I observed this nest; he fed the nestlings four times, a rate normal for monogamous males (Chapter 24). Another male in the identical situation behaved in much the same way.

Two males had young that had been out of the nest 1–2 days when the second female began building. Each male gave about equal attention to the fledglings and to the building female, behaving normally for each situation.

Two males were deserted by one mate at the time the second was building (desertion following nest predation). One male disregarded the building female during many hours that I watched on all 3 days of active building; he advertised constantly and acted as though unmated. The other gave his full attention to the building mate from the moment the second disappeared.

Monogamous males with first brood out of nest.—As would probably be expected from the foregoing, some monogamous males were attentive both to first-brood fledglings and to the female when she was building a second-brood nest (see also p. 267). Others, however, appeared to leave the care of the first brood to the mate and to give full attention to observing her as she built.

An idea of the time allocation of monogamists that were attentive both to young and the mate is suggested by the following: I watched the female working on the nest on the second day of building. The male came near the nest and sang for 1–3 min five times during 2 hours in the late morning. Next day (which was not the final day of building), he did the same six times during 1.5 hours. Most of the rest of the time he tended the fledglings (four, 18–19 days old); the female also tended them at times.

In contrast, on a territory on which I spent 15 hours observing building of the second-brood nest, I tried persistently to see the male feed (one fledgling, 7 days old) but saw no sign of this. He was extremely attentive to the female and her nest building. She fed the young until she began to incubate, when the male took over its care.

Once both the male and the building female ignored grown but dependent fledglings 34 days old, which gave hunger calls constantly; one young followed a strange, intruding male and begged. The young disappeared from the territory after age 34 days, suggesting an abbreviated period of dependence (see Chapter 28); but they survived. One was seen at age 41 days, one at age 72 days.

CHAPTER 17

TEMPORAL ASPECTS OF NEST BUILDING

TIME REQUIRED TO BUILD FIRST-BROOD NESTS

Nest building is divided into an active and an inactive phase. The first ended when the nest appeared functionally complete and when steady, active, building was replaced by desultory and occasional building trips. The inactive phase ended with the close of the day before egg 1 was laid. In combination the two phases make up the building interval. The number of building trips per unit of time yields a building rate, and spacing of trips is the building rhythm.

Data on the length of the building interval and its phases have been taken only from nests low enough to permit close inspection. Most nests that the Brown-headed Cowbird parasitized were rejected because the cowbird's habit of removing a host egg often made it impossible to be sure that the first warbler egg observed was the first egg laid.

Hours at which nests were begun.—Most statements about the hour a female began to build are based on two visits to a territory, between which building started. No nest is known to have been begun before 0800 or after 1500. Two females began small fragments (Chapter 12) at 1600 and 1625, respectively, but did not resume them next day.

Of 21 nests whose beginning times I know (margin of error about 30 min), 16 were distributed 4 each among the hours 0800–1200. Of the others, 3 were started between 1200 and 1300, 1 between 1300 and 1400, and 1 at about 1500. In addition, the beginning time of 15 nests is known with a margin of error slightly greater than 30 min; 6 were certainly begun before 1200 and 4 after 1200; 5 were begun between 1000 and 1400. Thus the start of building of 31 nests can be assigned to either morning or afternoon; 22 (71%) were begun before 1200, and most of the remaining 9 were begun within 1–2 hours after 1200.

Working hours during active building.—From first light until nightfall, I watched construction of two nests on both days 2 and 3 (the final day) of building; both had active phases of 3 days. Table 47 summarizes the data. One of the females made her first building trip at 0534 on day 2 and at 0557 on the final day; these times were 44 and 67 min after civil twilight. The other began to build at 0812 on day 2 and at 0647 on final day, 202 and 117 min after civil twilight. No reason for the differences in timing of these individuals was apparent. On eight other occasions I saw females working on nests between 0550 and 0640; they may have made still earlier trips. Another female on day 2 of building made her first building trip at 0745. Therefore the case, above, of the bird that started at 0812 is probably somewhat unusual.

Eight times, all in good weather, I saw females make the day's final building trip (Table 48). It will be noted that building stopped about 30 min before males quit singing (compare Table 48 with Fig. 9). In the case of female F (Table 48), which made her last trip at 1940, I also happened to see her mate go to roost,

TABLE 47
BUILDING TRIPS¹ PER HOUR ON SECOND AND THIRD² DAYS OF BUILDING BY TWO FEMALES

	Time	Female A		Female B		Time	Female A		Female B		Time	Female A		Female B	
		4 June	5 June	29 June	30 June		4 June	5 June	29 June	30 June		4 June	5 June	29 June	30 June
Time of first trip		0812	0647	0534	0557		0812	0647	0534	0557		0812	0647	0534	0557
Time of last trip		1851	1841	1928	1902		1851	1841	1928	1902		1851	1841	1928	1902
Analysis per hour ³	0600					0900					1200				
Trips		0	0	6	3		10	4	27	2		0	1	13	6
Sec at nest/trip															
Extremes		—	—	5-60	16-138		10-280	30-140	8-85	6-7		—	15	6-135	7-51
Mean		—	—	42	69		70	91	25	7		—	—	42	19
Min at nest															
Total		0.0	0.0	4.2	3.5		11.7	6.1	11.4	0.2		0.0	0.3	9.1	1.9
% hour		0	0	7	6		20	10	19	0+		0	0+	15	3
Analysis per hour ³	0700					1000					1300				
Trips		0	2	9	4		10	3	22	3		13	1	11	1
Sec at nest/trip															
Extremes		—	45-430	7-100	18-102		15-70	20-35	5-81	39-63		5-136	15	12-88	52
Mean		—	38	41	49		38	28	27	47		38	—	31	—
Min at nest															
Total		0.0	1.3	6.1	3.3		6.3	1.4	10.0	2.4		9.4	0.3	5.7	0.9
% hour		0	2	10	6		11	2	17	4		16	0+	10	2
Analysis per hour ³	0800					1100					1400				
Trips		4	5	22	8		4	0	15	5		8	2	9	7
Sec at nest/trip															
Extremes		17-32	33-512	5-72	6-41		15-30	—	6-95	29-76		14-230	40	5-95	7-58
Mean		24	150	21	26		20	—	32	45		50	40	34	29
Min at nest															
Total		1.6	12.5	7.8	3.4		1.3	0.0	8.0	4.5		6.7	1.3	5.1	3.4
% hour		3	21	13	6		2	0	13	8		11	2	9	6

TABLE 47 Continued

	Time	Female A		Female B		Time	Female A		Female B		Time	Female A		Female B	
		4 June	5 June	29 June	30 June		4 June	5 June	29 June	30 June		4 June	5 June	29 June	30 June
Time of first trip		0812	0647	0534	0557		0812	0647	0534	0557		0812	0647	0534	0557
Time of last trip		1851	1841	1928	1902		1851	1841	1928	1902		1851	1841	1928	1902
Analysis per hour ^a	1500					1700					1900				
Trips		10	2	8	2		2	1	1	2		3	1	4	1
Sec at nest/trip															
Extremes		10-100	30-185	7-107	20-84		19-30	34	7	30-100		12-30	75	12-55	26
Mean		42	103	33	52		25	-	-	65		22	-	24	-
Min at nest															
Total		6.9	3.6	4.4	1.7		0.8	0.6	0.1	2.2		1.1	1.3	1.6	0.4
% hour		12	6	7	3		1	1	0+	4		2	2	3	1
Analysis per hour ^a	1600					1800					Summary				
Trips		3	1	4	3		4	1	5	2		71	24	156	49
Sec at nest/trip															
Extremes		40-48	33	9-97	17-42		10-30	30	10-125	20-30		5-230	15-512	5-135	6-138
Mean		43	1	35	29		22	-	56	25		41.8	90.0	30.9	37.0
SD												45.5	138.0	27.9	27.0
Median												30	38	21	30
Min at nest															
Total		2.1	0.6	2.4	1.4		1.5	0.5	4.7	0.8		49.4	36.8	80.6	30.0
% hour		4	1	4	2		3	1	8	1					
% interval between first and last trips of day												7.7	5.2	9.7	3.8

¹ A building trip is a trip to the nest with material.² The active phase at both nests was 3 days; day 3 was the final day of active building.³ Hours were measured from 30 min before the designated time until 30 min after that time; thus 0700 began at 0630 and ended at 0730.

TABLE 48
TIME OF FINAL BUILDING TRIP OF DAY¹

Female	Date	Stage of building	Last trip	
			Time	Minutes before civil twilight
A	4 May	Day 2	1911 ²	60
B	7 May	Day 2	1845	89
C	4 June	Day 2	1851	108
C	5 June	Day 3 ³	1841	118
D	22 June	Day 3 ³	1915	93
E	29 June	Day 2	1928	92
E	30 June	Day 3 ³	1902	116
F	4 July	Day 4 ⁴	1940	67

¹ All data refer to the active phase of building.

² This female returned to the nest at 1914 but brought no material.

³ This was the final day of active building.

⁴ This was a second-brood nest, on which building proceeded slowly (see page 167). Its condition at the end of day 4 was approximately that of first-brood nests at the end of day 2.

at 2019, 28 min before civil twilight. Assuming that females and males roosted at about the same time, these facts suggest that females stopped work on the nest some 30–70 min before roosting.

Females C and E (Table 48) quit work only slightly earlier on the final day of active building than on the preceding day; I believe that in general females continued to build until evening on the final day, that is, they did not evaluate the nest and terminate building whenever it was complete, e.g. at midday. In addition to the frequent building trips observed late on the final day, the following evidence indicates that many aspects of active building behavior were geared to day-long units of time: (1) The building rate declined on day 2 of the active phase, apparently regardless of how much work the female had done on day 1, i.e. regardless of the hour at which she had begun to build on day 1. (2) Females seemed not to prolong building to compensate for working time lost during rains of a few hours' duration (p. 156). (3) Experimental alteration of the nest had no apparent effect on the amount of work subsequently performed by some females (p. 156; see also p. 162).

Minimum duration of active building.—First nests of the season were larger than later nests (Chapter 15), and it will be seen below that they took longer to build. Therefore data on minimum duration of active building are provided by replacement nests built in favorable weather. One nest, at which I watched almost every building trip, was completed about 62 hours after it was begun; excluding dusk and darkness, it took about 36 hours to build. Two other nests for which my observations were nearly as complete took about 54 and 60 hours of elapsed time, 32 and 33 hours of working time. In 2 additional cases nests appeared complete in the late morning, after 46 and 69 elapsed hours; but if the females kept building until dusk, as the evidence suggested, elapsed times of construction were about 53 and 76 hours and working times about 31 and 43 hours.

Progress of construction, according to hours spent working.—Numbers of working hours necessary to bring nests to various stages of completion can be stated roughly, but differences in nest size and in hour of beginning to build produced considerable variation. The generalizations are based only on replacement nests,

TABLE 49
DURATION¹ OF BUILDING INTERVALS AND PHASES,² ACCORDING TO DATE

Cases, by Date Nest was Begun												
Duration ¹ of active phase ²	25 April- 15 May		16-31 May		1-15 June		16-30 June		1-19 July		Totals	
	N	%	N	%	N	%	N	%	N	%	N	%
3	7	10	22	65	25	69	21	91	5	100	80	46.8
4	36	49	11	32	11	31	2	9	0	0	60	35.1
5	19	26	1	3	0	0	0	0	0	0	20	11.7
6	6	8	0	0	0	0	0	0	0	0	6	3.5
7	2	3	0	0	0	0	0	0	0	0	2	1.2
8	3	4	0	0	0	0	0	0	0	0	3	1.8
Totals ³	73	100	34	100	36	100	23	100	5	100	171	100.0
Median	4.3		3.3		3.2		3.4		3.0		3.59	
Mean	4.6		3.4		3.3		3.1		3.0		3.82	
SD	1.1		0.6		0.5		0.3		0.0		1.04	
Duration ¹ of inactive phase ²												
0	2	2	0	0	2	5	2	7	1	17	7	3.1
1	18	17	26	54	28	67	22	79	5	83	99	43.4
2	38	37	16	33	10	24	3	11	0	0	67	29.4
3	28	27	5	10	2	5	1	4	0	0	36	15.8
4	14	13	1	2	0	0	0	0	0	0	15	6.6
5	3	3	0	0	0	0	0	0	0	0	3	1.3
8	1	1	0	0	0	0	0	0	0	0	1	0.4
Totals ³	104	100	48	100	42	100	28	100	6	100	228	100.0
Median	2.3		1.4		1.2		1.1		1.3		1.62	
Mean	2.5		1.6		1.2		1.1		0.8		1.86	
SD	1.1		0.8		0.7		0.6		0.2		1.11	
Duration ¹ of building interval ²												
3	0	0	0	0	1	3	0	0	0	0	1	0.5
4	4	6	12	32	21	55	17	71	5	100	59	30.6
5	9	10	16	43	14	37	5	21	0	0	44	22.8
6	18	20	5	14	2	5	2	8	0	0	27	14.0
7	22	25	4	11	0	0	0	0	0	0	26	13.5
8	16	18	0	0	0	0	0	0	0	0	16	8.3
9	12	13	0	0	0	0	0	0	0	0	12	6.2
10	6	7	0	0	0	0	0	0	0	0	6	3.1
over 10 ⁴	2	2	0	0	0	0	0	0	0	0	2	1.0
Totals ³	89	100	37	100	38	100	24	100	5	100	193	100.0
Median	7.1		5.6		4.4		4.2		4.0		5.33	
Mean	7.2		5.0		4.4		4.4		4.0		5.82	
SD	1.7		1.0		0.6		0.6		0.0		1.86	

¹ Measurement is in days; a fraction of a day is treated as a whole; e.g., a nest begun at 1200 on 3 June and substantially completed at 1200 on 6 June is treated as having taken 4 days of active building; see page 152.

² The building interval started with the day on which building began and ended with (included) the day before egg 1 was laid. Phases of this interval are described on page 149.

³ Half-monthly percentages were rounded and do not always total 100.

⁴ One interval was 11 days and one was 14 days.

because of the greater variability in the active phase of first nests implied by the data according to date in Table 49. After 4 hours, most nests were slightly concave disks 3-5 cm in diameter. Rather uniformly, 13-16 hours were required to produce a thin shell with walls of full height (when the nest was built in that order; see Chapter 15). Thickening with stiff material usually took 4-5 additional hours.

Padding began some 18–21 hours after construction started and took only 5–7 hours in nests that were completed in the minimum time (3 days). Some nests had much padding but little lining, while in others the proportions were the opposite. Insertion of lining usually required 7–13 hours; one nest was lined in 5 hours.

Duration of active and inactive phases and of building intervals, in days.—With most nests, it was possible to determine only the days on which building began, on which the active phase ended, and on which egg 1 was laid, or some two of these days. Therefore, time is measured in calendar-day units, i.e. fractions are rounded upward.

Shown in the 2 right-hand columns of Table 49 are durations of 171 active phases, 228 inactive phases, and 193 building intervals. Omitted is a case in which the female suspended building, produced and laid in a complete nest, and later resumed work on the nest whose building had been interrupted.

Length of the inactive phase varied more than that of the active phase (coefficient of variation of the former, 60%; of the latter, 27%). Lengths of the two phases were positively correlated (testing by Spearman's rank correlation, $P < 0.01$). In two exceptional cases, nests had 8-day and 7-day active phases but only 1-day inactive phases; similarly a few had active and inactive phases each 3 days long.

Date and duration of building.—Table 49 shows that the duration of the building intervals and its phases tended to become shorter as the season progressed. Kruskal-Wallis analyses of variance by ranks of the half-monthly data for the building interval and both its phases produce H values significant beyond the 0.001 point.

Doubtless more than one factor was responsible for the prolonged early-season interval between beginning of building and of laying. The active phase was probably longer because first nests were larger, but it is also likely that females varied physiologically with date (independently of weather from day to day; see p. 156) and that many were not in condition to build rapidly when they started building. Thus, relative date of beginning of building and length of both active phase and of building interval were negatively correlated, as the last-mentioned hypothesis would predict. Treating the day on which the first female began to build each year as day 1, the following day as day 2, etc., and applying Spearman's rank correlation test to 79 first nests of the season, r_s for date of beginning to build and duration of active phase was -0.23 ; $t = 2.07$; $df = 77$; P one-tailed < 0.025 . In a test of association of date and duration of building interval, $r_s = 0.21$; $t = 1.89$; $df = 77$; P one-tailed < 0.05 .

Number of nests built by individual and duration of building.—Table 50 distributes building intervals of 122 nests according to the rank of each in the series of nests built by the individual female in a single season. (Ages of builders are also shown and will be discussed later.) Clearly, first-nest intervals were longer than those of later nests; second-nest intervals may have been longer than those of later nests. In a Kruskal-Wallis analysis of variance, H is significant beyond the 0.001 point. Both active and inactive phases of first nests were longer than those of subsequent nests. For example, the median active phase of first nests was 4.3 days, of second nests 3.4 days; and the respective median inactive phases of these two groups were 2.7 and 1.4 days.

TABLE 50
DURATION OF BUILDING INTERVAL,¹ ACCORDING TO AGE OF FEMALE²
AND NUMBER OF NEST IN SEASON'S SEQUENCE

Duration of building interval, days ¹	Nest 1			Nest 2			Nest 3			Nests 4-9			Total	
	Y	O	Total	Y	O	Total	Y	O	Total	Y	O	Total	Y	O
4	2	2	4	3	7	10	3	6	9	1	4	5	9	19
5	2	7	9	3	8	11	0	3	3	2	4	6	7	22
6	6	7	13	1	3	4	0	0	0	0	0	0	7	10
7	8	11	19	1	0	1	0	0	0	0	0	0	9	11
8	6	8	14	0	0	0	0	0	0	0	0	0	6	8
9	2	7	9	0	0	0	0	0	0	0	0	0	2	7
10	0	3	3	0	0	0	0	0	0	0	0	0	0	3
Over 10	0	2	2	0	0	0	0	0	0	0	0	0	0	2
Totals	26	47	73	8	18	26	3	9	12	3	8	11	40	82
Median	6.9	7.2	7.0	4.8	4.8	4.8	4.0	4.3	4.2	4.8	4.5	4.6	6.1	5.5
Mean	6.8	7.3	7.1	5.0	4.8	4.8	4.0	4.3	4.3	4.7	4.5	4.5	6.1	6.2
SD	1.3	2.0	1.8	0.9	0.8	0.8	—	—	0.5	—	—	0.5	1.6	2.0

¹ Measurement is in days. A fraction of a day is treated as a whole; see footnote 1, Table 49. The building interval started with the day building began and ended with (including) the day before egg 1 was laid.

² Only females that could be aged either as yearlings (Y) or as older than yearlings (O) are included.

The foregoing results were to be predicted from the change in duration of the building interval according to date; the further question is whether the two factors (date and nest number) were independent. Statistical tests revealed no independent effect of nest sequence.

Age of builder and duration of building.—Building intervals of individual females did not vary according to whether they were yearlings or were older than 1 year (Table 50). Interestingly, 26 yearling females built the first nests of their lives in a median 6.9 days, in comparison with 7.2 days for first nests of the season of 47 older females. Nests of yearling females were not distinguishable in appearance (see p. 125).

Nest size, climate, and duration of building.—Early nests may be bigger, and for that reason take longer to build, because it is adaptive to install more insulation against cold. Between 25 April, the earliest date a nest was begun, and 19 July, the latest date, the long-term daily mean temperature at Bloomington rises from 13.3°C to 24.4°C (Visser 1944: 476). This suggestion of a climatic effect may require reconciliation of the facts that the long-term temperature becomes warmer gradually, whereas the change in nest size and duration of building is abrupt (see p. 125 and Table 49). Possibly the reconciliation is that the large size of first nests could be an adaptation against spells of severe cold rather than against normal seasonal temperatures (compare Tinbergen 1957: 25). I have found no long-term records showing distribution of dates of extreme cold; but during the study, daily minimum temperatures fell below 4.4°C on 37 days between 25 April and 15 May, as opposed to only 14 such days in the period 16 May–31 May and none thereafter. Two days prior to 16 May registered minima between –3.9°C and –1.7°C; none did so after 15 May.

Photoperiod and duration of building.—The period of daylight is shorter at the beginning of the breeding season (see Figs. 8 and 9). Therefore unless the daily

building rate was faster at early nests, they should take longer to build even in the absence of a size difference.

Weather and duration of building.—Bad weather appeared to affect the length of the building interval (as opposed to the beginning of building; see Chapter 13) only when it was unusually severe or prolonged. The longer active phase of early nests sometimes appeared attributable to bad weather, which was more frequent in late April and May than thereafter and caused females to slow down or interrupt work. In one test of this possibility, I classed building intervals that lasted at least 9 days as unusually long (see Table 49) and examined weather records during 18 such long intervals (all for which information was available). The following episodes are suggestive because, in each, two females prolonged building. (1) Two females began to build simultaneously; 6 successive cold days (daytime maximum always below 21.1°C) followed, beginning on day 2 of building. One female had an 8-day active phase and 2-day inactive phase; the other had a 5-day active and a 5-day inactive phase. (2) Two females began to build; a little later that day it started to rain, and 20.5 cm of rain fell over days 1 through 5 of building. One female quit working after the second rainy day and resumed 5 days later; her building interval was 14 days. The other built slowly for 8 days, then had a 1-day inactive phase. However, one long building interval fell during wholly favorable weather, and bad weather did not always retard the building rate.

Evidence that bad weather slowed rate of growth of follicles and retarded ovulation is reported in Chapter 20; any such effect prolonged the inactive phase and therefore the building interval. (Compare Brimley 1891, Stanwood 1910b, Mousley 1928, Hann 1937: 168, Schrantz 1943: 370, Mayfield 1960: 72–73. Burleigh 1927 reports the remarkable case of a Pine Warbler that began to build its first nest on 17 February and that laid egg 1 on 15 March; snow fell on 2 March.)

Statistical analyses to learn whether the variation in length of active phase at nests with phases of 3, 4, and 5 days was associated with different temperature and precipitation conditions during building produced nonsignificant values. Since some females interrupted building during rainfall, I searched for explanations for this apparent absence of effect of weather on active phases. One possibility is that females speeded up the building rate when the weather improved. I sometimes detected bursts of unusually fast building following interruption of work by rain (see pp. 163, 165), but the point cannot be substantiated statistically. A second possibility is that females quit building, i.e. treated the nest as complete, even though it contained less material than it would have if weather had not interrupted building. Evidence that females will lay in an incomplete nest comes from an experiment in which I removed large amounts of material from a nest at three different times during the padding stage. The total quantity taken probably represented 5 hours of work by the female; and the final removal was at 1630 on day 2 of building, too late for her to compensate by increasing her building rate that day. Nevertheless she began to line the almost unpadded nest next morning and finished it that day. Obviously, in this experiment the female went through the complete performance of building a nest, which distinguishes the case from that of a female whose building is interrupted by bad weather. However, in Hinde's (1965: 386–388) experiments with canaries, building decreased rapidly at about the time laying began, even in females that were not permitted to complete nests.

(Some of my experiments described on pp. 158–159 suggest that elapsed time from start of building, not the condition of the nest, was the more important fact in determining length of the active phase; see also p. 162).

Other factors possibly affecting duration of building.—A relationship might conceivably be found between a female's date of pair formation in spring and length of building interval of her first nest, but statistical tests of this point proved negative. Analysis also revealed no relationship between length of the individual's pre-nest-building period and building interval. Interestingly, the building interval of replacement nests proved not to be affected by the stage at which the predecessor nest had failed. Also negative were tests to determine whether individual females tended to be slow or fast builders.

TIME REQUIRED TO BUILD FIRST NESTS OF PAIRS FORMED IN MIDSEASON AND SECOND-BROOD NESTS

First nests of pairs formed in midseason.—Females that paired in midseason (defined on p. 89) probably had nested previously in the same year (Chapters 30 and 31). Active phases of 10 nests of such females, all of which paired after 1 June, were uniformly 3 days long. Of 11 known inactive phases, 5 were 1 day long, 1 was 2 days, and 3 were 3 days; two females had no inactive phase, i.e. laid the day after active building ended. Of 10 known building intervals, 2 lasted 3 days, 5 lasted 4 days, 1 lasted 5 days, and 2 lasted 6 days.

Inactive phases of the first nest built after midseason pair formation may have been longer than inactive phases of replacement nests built by females that did not switch mates. Table 49 shows that only 3 of the 76 inactive phases of nests begun after 31 May lasted as long as 3 days; all 3 cases are from the small sample ($n = 11$) of females that paired in midseason. And whereas 4 of 11 first nests built after midseason pair formation had inactive phases at least 2 days long, only 12 of 65 replacement nests built in June and July by females still mated to their original mates of the year had inactive phases 2 days long. If inactive phases of nests of late-formed pairs did in fact tend to be longer, two conjectural explanations come to mind: (1) Some females that left males in midseason may have done so because those females were temporarily incapable of reproduction; if so, residual effects may have been present even after they paired again. (2) Possibly a female, even in full breeding condition, was less capable of immediate sexual response to a male she had just paired with. A color-banded female whose mate deserted her during incubation paired with a neighbor the day after her nest failed, and she began to build that same day. Although this suggests she was in full breeding condition, her inactive phase was 3 days. Kendeigh (1941: 44), writing of House Wrens, states that a longer time may usually be required to attain the requisite emotional or physiological state for copulation "both for a first mating early in the season . . . and for a later mating in July. . . ."

Second-brood nests.—Second-brood nests were infrequent and often too high to permit close examination. One nest had an active phase of 5 days, 2 had inactive phases of 4 days, and 1 of 3 days. Interruption of work to feed the first brood appeared to slow down the building of two of these (p. 167). One female that probably did not feed fledglings had a 3-day active and a 1-day inactive phase.



FIGURE 11. Complete nest built in another complete nest experimentally introduced shortly after the female began to build. See text. The white line is a loosely tied string placed around the rim of the introduced nest; the constriction is natural. Above the string is part of the later nest. (Photograph by William C. Welborn, Jr.)

The other had a 4-day active phase (but lost time by simultaneously building the nest and a large fragment) and no inactive phase.

EXPERIMENTS ON DURATION OF BUILDING

Nest substitution.—I removed three nests under construction and substituted complete nests, doing so unobserved at night. Unless the contrary is stated, weights mentioned were taken in winter after storage in dry conditions; compare the experimental weights and measurements with normal data (Tables 39 and 40).

(1) A female's second nest was emptied by a predator on 8 June; she began replacement on 10 June and by evening had built an incomplete shell (1.4 g), which I replaced that night with her second nest (about 3.5 g). She continued to build until dusk on 12 June, apparently unaffected by the fact that the substituted nest was complete. (I then removed that nest and replaced it with the complete nest of another female.) Laying began 15 June, so the active phase was 3 days, the inactive phase 2 days. The experimental, double nest (Figure 11) weighed 7.8 g; its overall exterior depth was 80 mm, interior depth 43 mm; at the time of substitution the exterior depth had been 54 mm, interior 43 mm. (2) Case 2 was essentially like the foregoing; building behavior continued although it had been rendered superfluous. The active phase was 3 days, the inactive phase 1 day. (3) On 11 June a female abandoned a nest after eggs disappeared. The replacement begun next day was a shallow early-stage outer shell (1.5 g) by nightfall, when I substituted the nest that had just failed (which was too wet to weigh; its exterior depth was 57 mm, its interior depth 37 mm). On 13 June the female was seen in the substituted nest three times, once body shaping, twice sitting motionlessly. No building trips were made during my intermittent watches. On 14 June the nest

showed little evidence of work since the substitution; the female had added only a thin lining (0.6 g), which did not quite fit and resembled a bowl placed in another bowl of different shape and smaller size. The nest was unchanged on 15 June; on 16 June, egg 1 was present. Thus, beginning with the start of the replacement nest the female had a building interval of 4 days, an active phase of probably only 2 days. The experimental nest weighed 5.0 g; its exterior depth was 60 mm, interior depth 33 mm.

When Hinde (1965: 386–391; see also Hinde 1967) presented female canaries with nest pans of varying size and/or texture, significant decreases occurred in frequency of building trips during intervals of exposure to cups having the characteristics of a nest. If my experiments are sufficiently related to be compared, two of three produced results unlike Hinde's, in that building behavior was not suppressed. But the fact that one female's building was affected suggests that stimuli from the nest are a factor in the change in the Prairie Warbler's behavior during building, as expected. (See Hinde 1961: 386–391, 404–407; see also Lehrman *et al.* 1961.)

Removal of material.—As described (p. 156), removal apparently had no effect on a female's behavior.

Introduction of nestlings.—I introduced nestling Prairie Warblers or nestling Field Sparrows into four nests under construction. For convenience I shall describe behavior of both members of the pair.

(1) On 1 July a female began her seventh nest of the year and on 3 July started to line it. She had had nestlings in one earlier nest. At 0840, I introduced a 6-day-old Prairie Warbler. At 0841 and 0916 the female brought grass but did not insert it, leaving after 45 sec and 4.5 min, respectively, spent perched on the rim. At 0936 and 0958 she brought grass and engaged in all normal building movements, disregarding the young bird. I left, returning at 1222. The male had begun to feed the nestling frequently and was still doing so at 2024, when I removed it to protect it against cold; the female had not been seen at the nest during three 30-min afternoon observations. I restored the young at 0455 on 4 July and returned at 0747 to observe. The female was not present but had laid egg 1. Thus the building interval was 3 days; only one normal (nonexperimental) interval among 193 cases was so short (Table 49). The male continued feeding, whereas at 0803 and 0810 the female brought nest material and built. Injury kept me out of the field until 7 July, when the female was on two eggs, the male carrying food near the nest and showing alarm as if the introduced young were nearby. On 8 July the female abandoned the nest and eggs. Her short building interval, her continued building after laying, and the small clutch of two eggs (see Chapter 18) all suggest disorganization of her behavior.

(2, 3) On 25 May a female was completing the outer shell when I introduced a 2-day-old Prairie Warbler at 1535. She returned to the nest at 1538 to chase a Field Sparrow, looked into the nest 30 sec, left, returned three times between 1540 and 1543 without material, and looked into the nest each time. At 1545 she resumed building. After three repetitions of building by her during 4 min, I removed the nestling to save it from chilling. In the other case a female ignored a 1-day-old Field Sparrow and continued lining her nest for 80 min until I removed the sparrow.

(4) On 29 May at 0746, a female began to line her second nest; her first had failed on 25 May after the eggs had hatched. I put a 2-hour-old Field Sparrow into the new nest. The female returned with grass at 0747, picked at the nest, and left after 1 min. At 0749 she returned with and appeared to deliver food, departed after 30 sec, and repeated this at 0751. At 0832 I substituted a 6-day-old Prairie Warbler. At 0845 the female returned with grass; its disposition was unseen. She perched on the rim 3 min, several times pulled violently at the nestling or its bands, at 0903 brought food. During the remainder of the day (90 min of observation) she engaged in normal food bringing. The male was not seen to feed, but he was perched on the nest rim at 1958. On 30 May the male fed and the pair behaved exactly like parents of a 7-day-old nestling. That night a predator took the nestling. The eggs that would normally have been laid in the nest were not found. On 1 June the female began a new nest.

For females, my introduction of nestlings into the incomplete nest produced a situation with no natural parallel, and the case of the female that quit building and began to feed is therefore especially interesting. For males, the simultaneous existence of nestlings and a nest under construction is not greatly different from the experience of some polygynists; monogamists too may have young at the same time nests (second-brood) are being built. Polygynous males were attentive to young in one nest while also showing normal interest in a second mate building a nest (p. 148). Emlen (1941), experimenting at nests of Tricolored Blackbirds, found that the female brought little if any food before she finished laying and that neither sex responded to nestlings during building. He suggested that sexual activity inhibits the feeding response. Clearly, this is not true of all Prairie Warblers. Note also that Prairie Warblers evidently differ from most birds in that they copulate after incubation has begun (see p. 229).

Introduction of fledglings.—Four times I placed single caged fledgling Prairie Warblers near nests under construction. Three females (none known to have nestlings or fledglings earlier in the season) continued building and ignored the begging young; the mate of at least one of these females fed the introduced fledgling. In the fourth case, the building female had fed nestlings until her most recent nest was destroyed by a predator. The introduced fledgling called loudly for 30 min while this female built, eliciting no response. Suddenly the female began an intense distraction display directed at me, and the male became excited. I retreated and the female quit building and went repeatedly to the caged fledgling, apparently feeding it.

For both a male and a building female, the presence of introduced fledglings created a situation that resembles the natural condition when a second-brood nest is being built. The amount of attention given first-brood fledglings varied after the female started her second-brood nest, as described elsewhere in this chapter. There were natural counterparts for all of the behavior observed in the experiments with fledglings.

Perhaps the most interesting of the results described in this section is the variability of reactions, showing that the behavior even of females was not under inflexible internal control. While two females that were diverted from nest building had recently cared for young (see Lehrman 1955, 1961: 1332–1340; Lehrman and Wortis 1960), some that were not diverted had also done so. Not sur-

TABLE 51
FREQUENCY OF BUILDING TRIPS,¹ ACCORDING TO TIME OF DAY AND
DAY OF ACTIVE PHASE²

Hour of day	Day of active phase					
	1			2		
	Min observed	Mean trips/hr	Mean min between trips ³	Min observed	Mean trips/hr	Mean min between trips ³
0530-0730	0	—	—	240	3.8	16.0
0730-1130	0	—	—	739	14.8	4.1
1130-1530	175	28.8	2.1	798	10.4	5.8
1530-1930	415	16.2	3.7	645	5.4	11.1

Hour of day	Day of active phase					
	3 ^a			final ²		
	Min observed	Mean trips/hr	Mean min between trips ³	Min observed	Mean trips/hr	Mean min between trips ³
0530-0730	0	—	—	240	2.3	26.6
0730-1130	72	13.3	4.4	480	3.8	16.0
1130-1530	124	11.1	5.4	480	2.8	21.8
1530-1930	70	9.4	6.6	480	1.5	40.0

¹ A building trip is a trip to the nest with nest material. This table is a composite of all observations of at least 60 min at nests, except second-brood nests, watched during good weather. See pages 161-162.

² The active phase is defined on page 149. See text, below, for the distinction between day 3 and the final day.

³ Time is measured between arrivals at the nest.

prisingly, males were more responsive than females to introduced young; male reproductive behavior is less varied and presumably requires less internal integration and sequencing.

NUMBER, RATE, AND RHYTHM OF BUILDING TRIPS TO FIRST-BROOD NESTS

Building trips per day during active phase.—I never counted all building trips on the day a female began her nest, but for two females I recorded all trips on days 2 and 3 (the final day) of building replacement nests with active phases of 3 days. As Table 47 reveals, female A made 71 trips and female B 156 trips on day 2. On the final day female A made 24 trips, 34% of the preceding day's number; female B made 49 trips, 31% of the preceding day's number (compare Mayfield 1960: 74).

I counted building trips of 11 females during periods lasting at least 1 hour, including the day-long watches just described. During the pooled 83 hours' observation the weather was mostly warm and fair; there were no prolonged or heavy rains. Table 51 presents mean number of trips per time of day (divided into intervals of 2, 4, 4, and 4 hours, in chronological order from 0530 to 1930); it also shows mean minutes between trips, distributed according to day of active building (a subject to be discussed below). The table distinguishes between day 3 and the final day of active building, according to whether the information was taken from a nest with an active phase lasting 3 days or 4 days: Building on day 3 at nests with 4-day active phases is tabulated in the column headed "3" whereas building on day 3 at nests with 3-day active phases is tabulated in the column headed "final."

The hourly rate of building was faster on the day the female started her nest

than at any subsequent time (Table 51; compare Lawrence 1953b); therefore if a female began to build in the morning, as was usual, the number of trips made on day 1 would usually be greater than on any later day. Chi-square tests of data from day 1 and day 2 show that in each 4-hour period after 1130 there were significantly more ($P < 0.01$) trips on day 1 than day 2; the same is true when the period 1130–1530 on day 1 is compared with 0730–1130 on day 2. (The period 0730–1130 on day 1 is not compared because few data were obtained; building usually began or was discovered after 0730).

The nests with 4-day active phases analyzed in Table 51 were first nests of the season. The data for these suggest no difference in number of building trips on days 2 and 3; if that is correct, it helps account for the fact that first nests were larger.

The building rate is presented in Table 51 according to day of building instead of stage of construction (e.g. outer shell, padding) because I believe the rate was less affected by the progress of the nest than by other factors, especially the female's condition. Reasons in addition to those already suggested in this chapter follow: (1) Although the degree of progress of the nest at the start of day 2 varied according to the hour at which building had begun on day 1, the building rate on day 2 appeared not to be correlated with nest condition. (2) As noted, rates of building on days 2 and 3 at nests with 4-day active phases appeared the same, but the progress of construction on those 2 days differed, often greatly. (3) During the day-long observations of females building on day 2, the transition from work on the outer shell to work on the padding did not correlate with change in hourly rate of building. An activity pattern associated with hour of day, not stage of nest, was probably largely responsible for the change in rate on those days (see below).

Daily number of building trips early in breeding season.—I believe that in many or most cases the number of trips per day to first nests of the year was smaller than to later nests built in comparable weather, for these reasons: (1) The interval between morning and evening civil twilights was shorter early in the season (e.g. on 1 May, 14 hours 48 min, on 15 June, 15 hours 58 min). (2) Early nests sometimes were built so slowly that I was uncertain whether progress had been made during the last 24 hours. The possible importance of the female's condition at this time for the speed of her building has been referred to (p. 154); it is also likely that females had to allocate more time and energy to finding food early in the season than later.

Number of trips required to build a nest.—To estimate the number of trips necessary to produce the nests that are the subject of Table 47, I have calculated the number of trips an average female might make on day 1 and added this to numbers observed on day 2 and the final day. Female A began to build at about 1000 on day 1 and quit at about 1900; her calculated number of trips that day is 210. On this assumption, she made about 305 building trips during active building. Female B may have made about 356 trips during her active phase (she built from 1230 to 1930 on day 1). Recalling that these two nests were replacements, the larger first nests must often have required at least 100 additional trips, a figure suggested by rates for day 3 in Table 51. (Compare Mousley 1926, Sturm 1945, and Mayfield 1960: 74.)

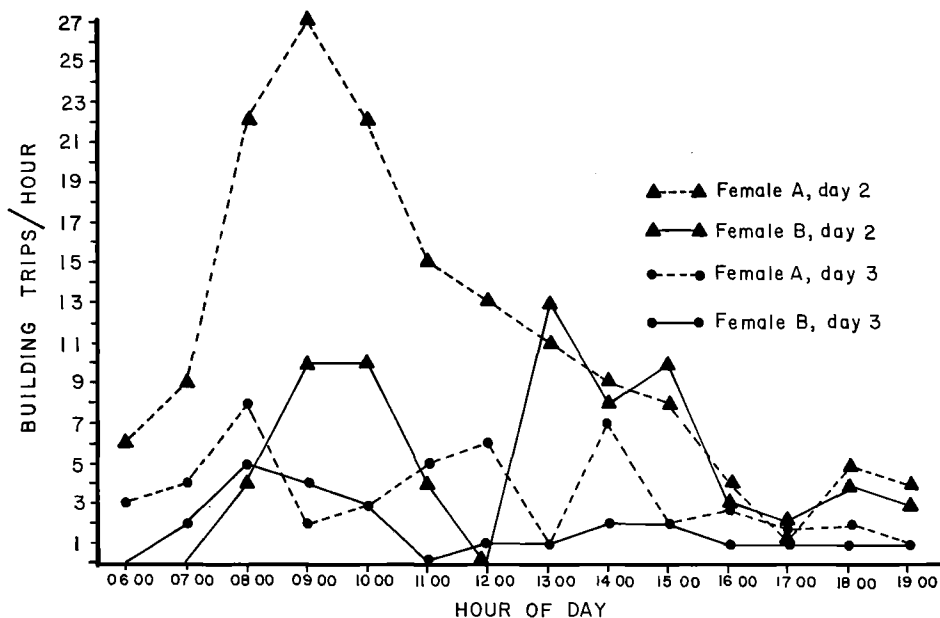


FIGURE 12. Number of building trips per hour to nest by building females on four day-long observations. Observations were on days 2 and 3 at replacement nests with 3-day active phases; see Table 47 and text. Time is eastern standard.

Distribution of building trips according to time of day.—This subject is analyzed in two ways: (1) Figure 12 shows trips per hour by the two females watched throughout 2 days. In the figure, each period begins 30 min before the hour and lasts 60 min; e.g. 0700 is the period 0630–0730. (2) The pooled data in Table 51 are assigned to four segments of the days of the active phase. The first segment is shorter than the others and ends at 0730; prior to that time, building was less frequent (pp. 149–151); the rest of the day (ending at 1930) is divided into 4-hour segments.

Morning counts on day 1 are lacking, but it seems unlikely that the morning rate could have been faster than that of the afternoon, considering the rapid rate of afternoon building.

Turning to day 2, despite substantial differences between the females watched all day, a few general similarities are apparent. Building started slowly, reached a peak about 0900–1000, and became substantially less frequent after 1100 (although female A later increased the number of trips). Activity was lowest at 1700 and revived slightly at the end of the day. The pooled data in Table 51 eliminate the irregularities seen in the hourly breakdowns in Table 47 and show a peak of building in the interval 0730–1130; the rate declined steadily in each subsequent 4-hour interval. A somewhat similar tendency is shown by brief observations on the third (not final) day.

On the final day female A made 12 trips between 0730 and 1030, quit building for 78 min, then made 1–2 trips each hour until the last trip, at 1841. Female B departed from her day 2 pattern and concentrated over half her work in the hours 0800, 1100, 1200, and 1400; but a rain during parts of the hours 0900

TABLE 52
NUMBER AND LENGTH OF INTERVALS AWAY FROM NEST¹ DURING FOUR
DAY-LONG OBSERVATIONS,² ACCORDING TO HOUR OF DAY³

Female A						
Hour ⁴	Day 2 of building, 4 June Min ⁵			Final day of building, 5 June Min ⁵		
	N	Extremes	Mean	N	Extremes	Mean
0600	0	—	—	0	—	—
0700	0	—	—	2	15.5–28.0	21.7
0800	3	4.5–6.0	5.5	5	5.5–19.0	10.2
0900	11	1.5–7.0	4.5	4	7.0–21.0	12.4
1000	10	0.5–10.5	5.6	3	14.5–77.5	43.5
1100	4	0.5–86.5	29.4	0	—	—
1200	0	—	—	1	62.0	—
1300	13	1.5–12.5	4.6	1	49.5	—
1400	8	1.5–14.0	6.1	2	11.0–52.0	31.5
1500	10	1.5–14.5	6.1	2	3.5–101.0	52.1
1600	3	4.5–24.0	16.8	1	5.0	—
1700	2	18.0–44.0	31.1	1	97.0	—
1800	4	1.0–60.0	16.6	1	32.0	—
1900	2	0.5–6.5	3.4	0	—	—
Summary						
N	70			23		
Median	5.0			15.0		
Mean	8.3			30.4		
SD	13.1			29.4		
Extremes	0.5–87.0			3.5–101.0		

Female B						
Hour ⁴	Day 2 of building, 29 June Min ⁵			Final day of building, 30 June Min ⁵		
	N	Extremes	Mean	N	Extremes	Mean
0600	6	3.5–15.5	9.2	3	8.5–15.5	11.7
0700	9	1.0–17.0	6.0	4	4.5–28.5	12.8
0800	22	1.0–17.0	2.4	8	2.0–15.5	7.6
0900	27	0.5–6.5	1.6	2	1.5–34.5	18.0
1000	22	1.0–8.5	2.3	3	3.5–10.5	6.3
1100	15	0.5–8.5	3.4	5	4.0–21.0	12.2
1200	13	2.0–6.0	3.8	6	4.5–23.5	10.0
1300	11	1.5–9.0	5.0	1	52.0	—
1400	9	1.0–14.0	6.2	7	1.5–17.5	9.1
1500	8	1.0–21.0	4.6	2	7.5–43.5	25.5
1600	4	1.0–53.0	20.0	3	16.5–27.5	21.1
1700	1	43.0	—	2	27.5–36.0	31.7
1800	5	3.0–27.0	11.9	2	20.0–57.5	38.9
1900	3	5.5–34.0	15.3	0	—	—
Summary						
N	155			48		
Median	2.0			10.0		
Mean	5.7			14.1		
SD	7.1			12.8		
Extremes	0.5–53.0			1.5–58.0		

¹ An interval away from the nest is measured from the time the female left until she returned.

² Data are taken from the days on which Table 47 is based. Together the two tables present the building rhythm.

³ When a period away from the nest began during one hour and ended during another, it is assigned to the hour in which it began.

⁴ Hours were measured from 30 min before the time shown until 30 min after that time; thus 0700 began at 0630 and ended at 0730.

⁵ Times are rounded to the half-minute.

and 1000 was probably responsible for reduced building at those times and, as suggested on page 156, may have led the female to accelerate building later in the day to make up for lost time.

Building rhythm.—For the four day-long watches, Table 52 gives numbers and lengths of periods away from the nest according to hour of day. When a female left the nest during one hourly interval and returned the next, the period away is assigned to the interval in which it began. Tables 47 and 52 when considered together provide a fairly complete picture of the rhythm of building by the two individuals dealt with.

Females building rapidly often made a series of quick trips, stayed away from the nest for one or more longer intervals, and then again made a series of closely spaced trips; Mayfield (1960: 74) has called such bouts of activity "work periods" in the Kirtland's Warbler. I shall use this term; but female Prairie Warblers did not always build in work periods, and Tables 47 and 52 are organized according to 60-min intervals.

As expected, absences tended to be briefest in the morning, longest at 1600 or 1700. Neither female went to the nest often enough to reveal a clear pattern of hourly variation in time at the nest per building trip. Female B showed some inclination to stay longer during the first 1–2 hours of the day's work, then to abbreviate stays to a minimum at 0800 or 0900; after midmorning on day 2 of building she tended to sit longer in the nest as the day advanced, until 1800 and 1900, when her stays became very brief. Both females were less prompt in leaving the nest on the final day of building than on day 2, not because insertion of lining required more time but because they sometimes sat quietly for a considerable period (maximum 8 min) after working. (At all stages of building females occasionally behaved in this way.)

An example of clearly defined work periods follows, with times rounded to the minute: On 29 June, 0633–0652, female B made 6 trips; the maximum time away from the nest was 6 min and the minimum 1 min. She then made 4 trips separated by 13, 10, 17, and 16 min; then 20 trips in 37 min (maximum time away 2 min); then stayed away 6 min, made 33 trips in 67 min; was gone 2 successive periods of 9 min each, made 13 trips in 28 min; was absent 8, 8, and 6 min between her next 3 trips.

On day 2 female A spent a total of 50 min, i.e. 7.7% of the time between the first and last building trips, at the nest (Table 47). Female B spent 81 min (9.7%) there. On the final day both females reduced time at the nest, female A to 30 min, 5.2% of the interval between first and last trips, and female B to 36 min, 3.8% of that interval.

During intervals of intensive building, the maximum time spent on the nest in any 60 min (Table 47) was 11.7 min by female A, 11.4 min by female B. Female A made only 10 trips during the 60 min referred to; the mean length of her stays was 70 sec. Female B, on the other hand, visited the nest 27 times and averaged 25 sec per visit. If work periods rather than arbitrary time intervals are considered, in a 67-min work period female B made 33 trips to the nest and spent 14.7 min (22% of the time) there; during a 37-min work period she made 20 trips and was on the nest 7.7 min (21%). Assuming that during such intervals as these no significant time was given to activities other than those di-

TABLE 53
FREQUENCY OF PRESENCE OF FEMALE ON NEST DURING INSPECTIONS¹
MADE IN INACTIVE PHASE,² ACCORDING TO TIME OF DAY

Time of day	Number of inspections	Females present	
		N	%
Before 0730	53	5	9
0730-0930	78	1	1
0930-1130	102	7	7
1130-1330	66	4	6
1330-1530	43	2	5
1530-1730	67	3	4
1730-dark	22	0	0
Totals	431	22	5.1

¹ Each time a nest was inspected to learn whether laying had begun, I recorded whether the female was present.

² The inactive phase of nest building is defined on page 149.

rectly involved in building, then gathering material and flying to and from the nest appear to consume nearly four times as much working time as insertion, shaping, and resting in the nest. As an estimate, on day 2 probably at least 75% of total time at the nest was spent in work, 25% in sitting quietly. On day 3, as noted, the percentage for working decreased.

Trips to nest during inactive phase.—Information on female visits during this phase was derived from (1) two long watches at nests with inactive phases lasting 1 day and (2) 431 records noting whether females were on nests when I visited these during the inactive phase. Some 300 nests supplied these latter data (Table 53).

(1) Long watches: From dawn to dusk on 10 June, I watched a nest (the builder's third of the season) begun 7 June and completed 9 June. The female went to it seven times, carrying grass on some and possibly all trips. Six trips fell in the period 0729-0834; the last was at 0927. Thus this female engaged in considerable building for about 1 hour; extreme lengths of stays on the nest were 30 and 200 sec, the mean 100 sec. On 1 July, from 0820 to 1120, I watched a nest begun 28 June and finished 30 June; the previous history of the female was unknown. She visited the nest at 0920 (brought material, built normally for 20 sec), 0937 (probably brought material, did not enter the cavity, perched beside the nest and worked on the rim 8 sec), and 1005 (brought no material, entered the cavity, worked briefly on the rim, sat quietly for 150 sec).

(2) Nest inspections: The nest inspections probably are a more reliable measure of average distribution of visits than are the two long observations of single individuals. Females were present on 22 of 431 inspections (5.1%), with no apparent variation according to date. It is not clear whether frequency of visits varied according to length of the inactive phase: On 221 inspections on day 1 of that phase, females were present 10 times (4.5%); on 130 inspections on day 2, 10 times (7.7%); on 80 inspections on day 3 or a subsequent day, 2 times (2.5%). The behavior described in the preceding paragraph indicates that visits to the nest during the inactive phase expressed a residual tendency to build. Therefore, possibly a large sample of data from nests with long inactive phases would show reduction of trips as the days passed.

Note that results of the 431 inspections are not consistent with those of the long observations in regard to time of day of visits. Inspections show female visits to the nest until late afternoon, with possibly no hourly variation (Table 53). The earliest observation of a female on her nest was at 0556, the latest at 1600.

RATE OF BUILDING TRIPS TO SECOND-BROOD NESTS

When the female tended fledglings (see p. 144), her building rate became unusually irregular; periods of concentrated rapid construction probably alternated with caring for the young. I counted building trips at two second-brood nests whose builders were also feeding first-brood young. Selected observations will be described.

(1) A female was discovered building the outer shell at 1015 on 24 June; she then made 10 building trips, each separated by 30–90 sec from the one preceding. This done, she flew toward calling fledglings and remained away from the nest 52 min, feeding the young at least part of this time. At 1124, she resumed rapid building and made nine quick trips. Next morning she was padding the nest and made only three building trips between 1015 and 1145. If the nest had been a first-brood nest, this would be a very slow building rate.

(2) A female began a second-brood nest on 1 July, was irregular in working, and took 5 days for active building. As the nest progressed she built more rapidly but continued to care for her one fledgling, probably without male help. Illustrative episodes: On day 2 between 0852 and 1000 she made 8 trips, on day 3 between 1015 and 1215 (the nest was still probably in the outer-shell state) 23 trips. When the fledgling begged, the female sometimes found food, fed it once, and resumed building; at 1155, she ignored it while gathering nest material 1 m from it but quickly returned and tended it until 1214; she then resumed building. Later this day she was seen foraging for herself at a remarkably fast rate, behaving like a female off the nest during incubation and probably for the same reason (p. 491). On day 4 between 0940 and 1110, she made 21 trips; the fledgling was not seen, but she fed it throughout the rest of the day.

CHAPTER 18

CLUTCH SIZE

Analysis is based principally on 188 selected nests whose contents were examined daily from building through laying, i.e. until at least a day of incubation had elapsed with no further egg being laid. Eggs were marked on the day they were laid. Clutches are assigned to the date on which egg 1 was laid. Nests found before building began but excluded from the sample were those parasitized by cowbirds, those in which laying apparently skipped a day (i.e. no new egg was found on a day between 2 days on which a new egg was found), those in which the female may have laid more than one clutch (five cases, discussed below), and those too high to see into. Seventy nests were found after laying began under circumstances indicating that clutches probably were complete; these provided information consistent with the data from the basic 188 nests and are used in one analysis.

The method of selecting the sample of 188 nests produces a bias in favor of small clutches, a point considered below.

As seen in Table 54, of the 188 clutches 14 (7%) contained 5 eggs, 139 (74%) 4 eggs, and 35 (19%) 3 eggs; the mean was 3.89 eggs (SD 0.50) and the median 3.92 eggs. Nest predation was heavy on the study area, with rates especially high during egg laying (Chapter 33); cowbird parasitism was, of course, largely concentrated during laying (Chapter 32). Bias toward small clutches is inescapable in these data because (1) only complete clutches can be used to determine clutch size; (2) more days are required to lay large than small clutches; and (3) increased duration of laying increases the risk of predation and parasitism (events that eliminate a clutch from the sample). Thus on a predator-free, cowbird-free study area more five-egg clutches would probably have been found.

No other students of the Prairie Warbler have published information permitting comparison of their data with mine, and the meager evidence is contradictory as to whether clutch size increases with latitude. Tending to show larger clutches in the north are reports from Michigan and New York. In Michigan, Walkinshaw (1959) found 5 clutches of 5 eggs and 6 of 4 eggs; Andrew J. Berger (pers. comm.) found 1 clutch of 4 and 1 of 5; and Wood (1951: 405) mentions only 2 clutches that can be regarded as complete, both of 5 eggs. Bull (1974: 505) states that 4 among 12 clutches discovered in New York contained 5 eggs, 5 contained 4 eggs, and 3 three eggs. Toward the south, on the other hand, Mengel (1965: 418) reports the mean size of 14 clutches from Kentucky as 3.5 (SD 0.14) eggs; no 5-egg clutches were found. In Tennessee, Albert Ganier (pers. comm.) discovered many Prairie Warbler nests, none of five eggs. The same is true of Merritt G. Vaiden and B. E. Gandy (pers. comm.) in Mississippi.

However, during a single season in Virginia, Jamison (1889) found 3 clutches of 5 eggs, 5 of 4 eggs, and 1 of 3 eggs, and also in other years observed 5-egg sets (but see Coues 1888, Kirkwood 1895: 358, Daniel 1901, and Bailey 1913:

TABLE 54
CLUTCH SIZES DURING HALF-MONTH INTERVALS, SOME ACCORDING TO AGE
OF FEMALES¹

Clutch size	Date on which egg 1 of clutch was laid					Totals	
	1-15 May	16-31 May	1-15 June	16-30 June	1-16 July	N	% ²
5 eggs							
All females	9	4	1	0	0	14	7
Old birds	5	2	0	0	0	7	8
Yearlings	0	0	0	0	0	0	0
4 eggs							
All females	35	60	26	13	5	139	74
Old birds	20	31	9	4	2	66	73
Yearlings	4	15	11	0	0	30	73
3 eggs							
All females	3	1	6	13	12	35	19
Old birds	0	0	2	6	9	17	19
Yearlings	2	1	3	4	1	11	27
Totals, all females	47	65	33	26	17	188	
Mean	4.1	4.1	3.9	3.5	3.3	3.89	
SD	0.5	0.3	0.4	0.4	0.5	0.50	
Median	4.1	4.0	3.9	3.5	3.2	3.9	

¹ Birds that laid 131 clutches could be aged; 57 clutches were laid by females of unknown age.

² Percentages indicate proportions of 5-egg, 4-egg, and 3-egg clutches laid by each class of female (all, old only, yearling only). Some percentages as rounded do not total 100.

304). Five-egg clutches are reported from Oklahoma (Nice 1931: 161), North Carolina (Pearson *et al.* 1919: 298), and Georgia (La Prade 1922; Burleigh 1958: 540; Burleigh's date, 5 August, is remarkable). See also the discussion on page 321.

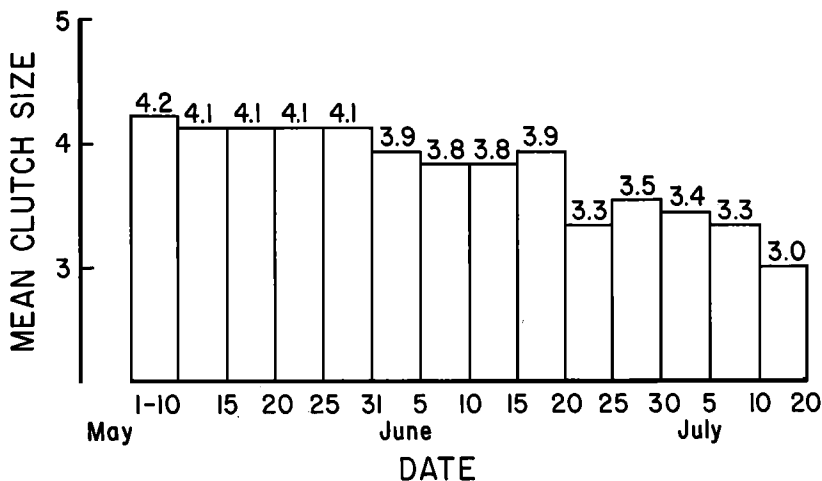


FIGURE 13. Mean clutch size, according to approximate 5-day intervals. First and last intervals are 10 days long to increase sample size. Clutches are assigned to the date egg 1 was laid.

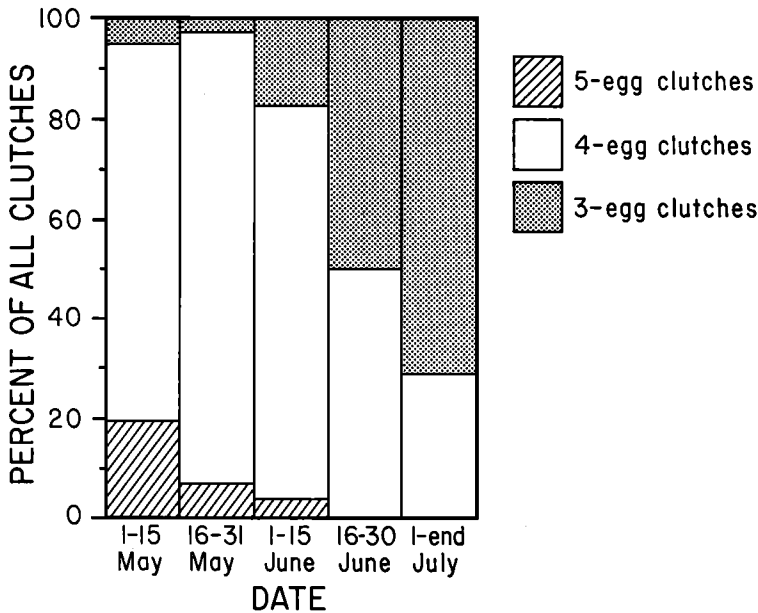


FIGURE 14. Clutch size, according to approximate half-month intervals. Clutches are assigned to the date egg 1 was laid.

FACTORS ASSOCIATED WITH VARIATION IN CLUTCH SIZE

Date, clutch number.—Clutch size fluctuated somewhat irregularly when the data are distributed according to 5-day calendar intervals (Fig. 13); but when the distribution is according to half-months (Table 54), it is apparent that size decreased during the season. In a Kruskal-Wallis one-way analysis of variance (not corrected for ties) of the data in Table 54, $H = 38.9$; $df = 4$; $P < 0.001$.

From beginning of laying until 15 June, at least 75% of all clutches consisted of 4 eggs (Fig. 14). In this interval a reversal in proportions of five-egg and three-egg clutches occurred, the former disappearing and the latter becoming more frequent. (The latest clutch of five eggs was begun on 1 June.) Between 16 June and the end of breeding, three-egg clutches predominated. (Compare Hann 1937: 172–173; Walkinshaw 1941, 1953; Stewart 1953; Mayfield 1960: 84–87.)

As expected, clutch size declined as nest number advanced, i.e. in the season's series of nests of individual females (Table 55). This decrease closely paralleled the decrease associated with date (Table 54). Sample size according to nest number is only 150, because numbers of nests built earlier by females that arrived on the study area in midseason were unknown; data from such females could not be used. Multivariate analysis does not disclose whether date and clutch number affected clutch size independently. If they did not, the possibility exists that clutch number and not date was critical and that the effort of building earlier nests and synthesizing eggs caused reduction in size of later clutches (compare Romanoff and Romanoff 1949: 57–58). However, von Haartman (1967: 160–162) discounts this "popular belief," at least with respect to some species. In the Pied Flycatcher in Finland he found no evidence that physiological exhaustion led to

TABLE 55
CLUTCH SIZE, ACCORDING TO NUMBER OF PREVIOUS NESTS¹ OF INDIVIDUAL

Clutch size	1st		2nd		3rd		4th		5th, etc. ²		Unknown	
	N	%	N	%	N	%	N	%	N	%	N	%
5 eggs	13	14	1	3	0	0	0	0	0	0	0	0
4 eggs	72	80	30	86	7	70	7	78	2	33	21	55
3 eggs	5	6	4	11	3	30	2	22	4	67	17	45
Total	90	100	35	100	10	100	9	100	6	100	38	100
Median		4.1		4.0		3.8		4.0		3.3		3.6
Mean		4.1		3.9		3.7		3.8		3.3		3.6
SD		0.4		0.4		0.5		0.4		0.4		0.4

¹ Nests built by individual females in single seasons were ranked chronologically. Nests destroyed before at least one egg was laid were not considered. Four second-brood nests are included.

² Included are two fifth nests, one sixth nest, one seventh nest, one eighth nest, and one ninth nest.

diminishing clutch size. "On the contrary, repeat clutches are small because they are laid late."

My evidence suggests that the smaller size of late clutches was not attributable to the burden of having laid prior clutches. Even in fourth nests, sets of four eggs constituted over 78% of the total. (The number of nests built and laid in by the average female per season was smaller than four; see Tables 133, 143, 144.) When third nests are subdivided according to date, the suggestion is clear that clutches in early third nests were larger than those in late third nests. To increase the sample for this analysis, I added 8 third clutches to the 10 shown in Table 55, obtaining these 8 from nests found after laying began (see p. 168). Distributing the resulting 18 third clutches among 3 calendar intervals, as in Table 56, all of 6 clutches laid prior to 6 June consisted of 4 eggs; 7 of 8 clutches laid 6–15 June consisted of 4 eggs and 1 of three eggs; and 1 of 4 clutches laid 16–30 June held 4 eggs, while 3 held 3 eggs.

Certain episodes also imply that exhaustion did not affect size of replacement clutches: A banded female lost nine nests either during the laying interval or immediately after laying full clutches. Predators and cowbirds were responsible for her earlier failures, and I took her subsequent clutches as soon as they were laid in order to learn how many nests and eggs she could produce. Prior to the day she began her sixth clutch (15 June) this female had laid 15 eggs, i.e. 2 full sets of 4 each and 3 incomplete sets. The sixth nest received 3 eggs, and she laid 3 additional clutches of 3 eggs for a total of 27 eggs that season. Other banded

TABLE 56
CLUTCH SIZE IN THIRD NESTS,¹ ACCORDING TO DATE²

Date	Number of cases, by clutch size	
	4 eggs	3 eggs
24 May–5 June	6	0
6 June–15 June	7	1
16 June–30 June	1	3

¹ The sample consists of nests known to have been the third in which the individual builders had laid at least one egg in the season involved. See text, this page.

² Clutches are assigned to the date on which egg 1 was laid.

TABLE 57
ANNUAL VARIATION IN CLUTCH SIZES IN FIRST NESTS

Year	Number of cases, by clutch size		
	5 eggs	4 eggs	3 eggs
1952	3	3	0
1953	2	3	0
1954	0	5	0
1958	1	11	0
1959	2	7	0
1960	2	11	1
1961	0	5	0
1962	1	10	0
1964	1	4	1

females built and laid in 7 and 6 nests, respectively, producing about 21 and 16 eggs. In sum, advancing date was associated with reduction in mean clutch size, probably without respect to the extent of the female's previous reproductive efforts (see King 1973: 88–96).

I have no evidence as to why clutch size decreased with date. The change may be an adaptation to the quantity or quality of food available in the last half of the breeding season, the possible effect of molt on parents of dependent young (see Chapter 41), and the fact that males sometimes desert and leave the young to the care of females late in the season (see p. 429 and compare p. 321).

Age.—Clutches of yearlings may have been smaller than those of older females, as is true in a number of species (see Lack 1966: 274, von Haartman 1967, Klomp 1970: 11–13). Table 54 shows sizes of 41 clutches laid by yearlings; the median is 3.82 eggs and the mean 3.73 (SD 0.45). This compares with a median of 3.92 eggs and a mean of 3.89 (SD 0.41) in 90 clutches of females at least 2 years old. In a Mann-Whitney *U* test, the value of $z = 1.62$; P (one-tailed) = 0.053. The proportions of 4-egg clutches of the 2 age classes were identical (73%); but no yearling laid a 5-egg set (except for a clearly anomalous case, p. 174), and only yearlings laid as few as 3 eggs in first clutches of the year. (Several three-egg sets laid in first nests by yearlings were observed after the study had ended and are not included in Table 54.)

Females exhibited too little site fidelity (Chapter 37) and too little variation in clutch size to yield satisfactory information about possible changes in clutch size as age advanced beyond 2 years. A bird at least 2 years old in 1961 laid 4 eggs in her first nest in that year and in 1962. In 1963, she laid 5 eggs in her first nest.

Individual differences.—The absence of site fidelity in most females prevented compilation of long histories of many individuals. One female laid 5 eggs in her first and second clutches in 1 year, thus accounting for 14% of all 5-egg clutches found. No other bird produced a replacement set of 5 eggs, and the date (1 June) of egg 1 in the second clutch of this female was 6 days later than that for any other 5-egg clutch.

Annual differences.—In considering whether clutch size varied annually, I have separated early from late nests and excluded the latter because breeding stopped earlier in some years than others (see Chapter 34). Early termination

TABLE 58
FIVE CASES OF ABNORMALITY IN EGG-LAYING RHYTHM AND NUMBER
OF EGGS LAID

Designation of female	Age ¹	Date of egg 1	Sequence of events by day, beginning with day egg 1 laid ²									
			1	2	3	4	5	6	7	8	9	10
A	old	11 June	E	O	O	E	E	E	E-I			
B	old	3 July	E	E	O	O	O	O	O	E	E	E-I
C	old	25 June	E	E	O	O	E	E	E-I			
D	old	27 May	E	O	O	E	O	O	E	E	E-I	
E	yearling	14 May	E ³	O	E	?	E ⁴	E	E-I			

E = egg laid O = no new egg present ? = no inspection I = incubation began

¹ Females older than 1 year old are considered old.

² The nest of female C was found on 26 June, with two eggs, laying dates unknown.

³ A cowbird laid an egg on 13 May. Cowbirds usually removed a warbler egg from a parasitized nest (Chapter 32); therefore a warbler egg may have been laid and taken before my inspections on 13 May, 15 May, or 18 May.

⁴ The new egg found on this date may have been laid the day before.

of breeding reduced the proportions of three-egg nests in such years. First nests of the season offer a more interesting problem, since 3-, 4-, and 5-egg clutches were laid in these and the effect of variation with date is reduced; but the number of first clutches that escaped predation and parasitism was small. Table 57 shows sizes of first clutches in years in which at least five data were available. Clearly, the variation may be attributable to sampling error, but differences seem suggestive. Assuming real differences, larger clutches tended to occur in years in which the first half of May, when many females began to lay, was warm. During the years of the study, average daily means for 1-15 May ranged from 21.2°C to 12.2°C. The warmest years were 1959, 1962, 1964, 1952, and 1953, in that order; all but 1962 ranked high in proportion of 5-egg clutches (Table 57). Furthermore, 1954, with no 5-egg sets, was one of the 2 coolest years (mean of both, 12.2°C). Even in 1960, the other cool year, special circumstances may account for the occurrence of 2 large clutches: egg 1 in each clutch was laid very late (25 May) after 10 days of hot weather.

ANOMALOUS CLUTCHES

In some or all of five nests females probably laid eggs that would normally have been elements of two distinct clutches. Rates of laying, dates, and ages of the females are summarized in Table 58. Details of selected cases are given below.

Female A: This female's first clutch had been abnormal in that four eggs were laid in three days (p. 189). I took these eggs on day 11 of the incubation period and substituted a set newly laid by another bird. She incubated nine more days, then deserted the substituted eggs (which were alive) and began a new nest the same day. Egg 1 was abnormally pale; no new eggs appeared for 2 days; she then laid 4 normally pigmented eggs, 1 per day. A predator destroyed the nest during incubation.

Female B: This female began a clutch on 3 July, laid again on 4 July, and on that evening was incubating at 1945, as is normal before the final egg is laid (Chapter 21). No egg was laid on 5 July, and the female was not found on the nest that day. On 6 July, she was on the nest, but had laid no new egg;

on 7–9 July she was not found on the nest, whose contents were unchanged. On 10–12 July she laid one egg each day and began incubating just before laying the final egg. The nest's height prevented my learning much of its subsequent history. Four eggs were present on 16 July; judged by their color, 2 were alive and 2 undeveloped. An egg hatched on 23 July and another next day; a predator then destroyed the nest.

Female D: This female laid 1 egg in her second nest, skipped 2 days and laid 1 egg, skipped 2 more days but incubated at times, then laid 3 eggs at the usual rate; during the laying of these 3 she probably did not incubate until just before the final egg. The nest was then emptied by a predator. Clutches in her four other nests were normal. (See the discussion, p. 187, of the possible effect of weather on this case.)

Female E: This yearling may have laid 5 or 6 eggs in her first nest, which was completed on 11 or 12 May and was parasitized by a cowbird on 13 May. The first warbler egg was found 14 May, the second 16 May. The nest was not inspected on 17 May; 3 warbler eggs and the cowbird egg were present on 18 May, and a new warbler egg was laid on each of the following 2 days. One egg disappeared 21 May; a second cowbird parasitized the nest on 26 May, causing failure.

RESPONSES TO INTERFERENCE DURING LAYING

Under natural circumstances Prairie Warblers are determinate layers. Loss of eggs before beginning of incubation never led to an increase in number of eggs laid, and introduction of extraneous eggs by Brown-headed Cowbirds did not lead to a reduction. Experimental introduction of two to four eggs, always introduced simultaneously rather than piecemeal, probably had no effect on size of the clutch subsequently laid.

Only selected instances of cowbird interference will be mentioned; female Prairie Warblers probably could discriminate between their own eggs and those of cowbirds (they often deserted; see Chapter 32), and behavior after cowbird laying may have involved reaction to the parasitization rather than simply to the number of eggs present. All cowbird interference and experiments to be referred to occurred either before laying began or during laying.

Natural egg loss.—Loss of an egg or eggs to predators, parasites, and tossing by the wind never led to the laying of more than four eggs. The only two variables observed in cases of egg loss were whether females continued to lay in the nest after the loss, and whether, if they did complete the clutch, they then incubated. Responses were much affected by the number of eggs that had disappeared.

In all instances (about 57) in which probably three eggs disappeared before the clutch had been completed, females deserted. (Numbers are approximate because often I did not know whether predation took place before or after laying the latest egg in the series.) However, in four of these cases, the females returned on the morning after predation and laid (dumped) an egg, which presumably had passed into the oviduct before predation (see p. 184).

In some 27 instances, I found the nest empty on the day on which egg 2 was

expected. Subsequent events were as follows: 20 females abandoned immediately; 4 laid 2 more eggs and incubated; 2 laid 1 more egg but did not incubate; 1 laid 2 more eggs but did not incubate.

In five cases, one marked egg disappeared during laying, and no cowbird egg was deposited. All 5 females laid the remaining eggs (for a total of 4); 4 females then incubated, but one did not. In addition, at 10 nests in which I was marking eggs as they were laid, the expected new egg was absent when I went to mark it. Probably all 10 had been laid shortly after dawn and had been taken before my arrival; the 10 females continued to lay and all incubated.

Experimental egg removal.—The foregoing evidence so uniformly indicated that females could not be induced to lay additional eggs that I performed only five removal experiments.

In four cases, I took egg 1 on the day it was laid. One female then abandoned; 3 laid egg 2, which in 2 of the cases I immediately removed. (A predator interfered at the other nest.) The birds whose egg 2 I had taken laid egg 3 in the still-empty nests; I took one egg 3 and left the other. Both females laid egg 4, which I left; one also laid egg 5 (on 14 May, a normal date for 5-egg sets). Neither bird incubated. Thus, removal of the first two eggs in one of these cases and the first three eggs in the other did not affect clutch size but led to desertion.

In the fifth experiment, I left egg 1 but removed each subsequent egg as it was laid. The female laid four eggs but did not incubate.

Nuttall (1832: 294–296) states that after he took 2 of 4 eggs from a nest, 2 more were added.

Introduction of eggs by cowbirds.—Not all cowbirds took eggs from Prairie Warbler nests that they parasitized (see Chapter 32). When they did not, and when the Prairie Warbler did not desert, there was opportunity to consider the effect of the extraneous egg on clutch size. Numbers of eggs the warblers might have laid cannot be known and the cases are too few to analyze statistically, but there is no indication that clutch size was modified. Extreme illustrations of this point follow: A female whose nest was parasitized the day she laid egg 2 laid 3 more eggs and incubated the 6 eggs in her nest. Another (female E, p. 174) laid and incubated at least five of her own eggs after a cowbird had introduced its egg; but other peculiarities suggest that the warbler in effect laid more than one clutch in the nest. The largest number seen in any nonexperimental nest was six eggs, in the two foregoing cases. Several females laid four eggs in nests containing a cowbird egg; not all incubated.

Experimental egg introduction.—I added eggs to 12 nests, but for various reasons (e.g. predation) only five experiments yielded information about the effect on clutch size. Field Sparrow eggs were introduced when Prairie Warbler eggs were unavailable; they resembled Prairie Warbler eggs, and nothing suggested that their use influenced results. The informative cases were as follows: In 3 nests I put 4 eggs, in 1 nest 3 eggs, and in 1 nest 2 eggs. All but one introduction was before the warbler had laid egg 1; in the exception, eggs were introduced just after the warbler had laid egg 1. The number of eggs laid in these nests was 3 in 3 cases, 4 in 2 cases. All females incubated. The largest number of eggs incubated was 7; the female laid 4 eggs in a nest into which I put 4, but 1 disappeared before incubation began.

CHAPTER 19

EGGS

GENERAL APPEARANCE

Color terms follow Palmer (1962: 4 and chart) unless otherwise indicated. To reduce subjectivity in matching eggs with the color chart, I obtained several independent judgments of egg color. Terms for shape follow Palmer (1962: 13–14).

Ground colors, texture.—Usual ground colors of freshly laid eggs were very pale cinnamon, pale cinnamon, pale smoke gray, very pale gray; occasionally they approached white; one female's eggs were pale bluish (not compared to color chart). In texture, newly laid eggs usually were hoary (frosted), sometimes slightly chalky. See also Bent (1953: 432). The yolk of fresh eggs was faintly visible through the somewhat translucent shell. After about 100 hours of incubation this translucence began to disappear in eggs that were alive; within another 24 hours the eggs were opaque. Associated with this change, some ground colors became very light gray, others almost white; a faint cinnamon cast continued on some. The texture at this time was lustreless or chalky; most eggs acquired a slight gloss, possibly through friction with the nest and contact with the female.

Spotting.—Figure 15 shows the approximate range of variation in spotting; occasional eggs had fewer spots. The commonest pattern of spotting (45–50% of the eggs examined) was a distinct wreath about one third the distance from the large end (Fig. 15, upper right egg) but occasionally nearer the midpoint between ends. Also a very common pattern (some 35% of the eggs) was a cap formed by spots on the large end, ordinarily covering about one quarter of the egg (Fig. 15, lower left egg). In both wreathed and capped patterns, usually a few finer spots were scattered over the remainder of the egg. In about 15% of the eggs the spots were not merged into a wreath or cap and were distinct and rather uniformly distributed (Fig. 15, lower right egg). Most spots were more or less rounded; thin straight streaks and scrawls were rare. See also Bent (1953: 432).

Spots of eggs that were compared to the color chart were one or more of four colors: light chestnut, medium chestnut, deep chestnut, blackish brown. In the field with no chart available, I judged some spots to be brownish olive, buffy brown, brownish red, and tawny. Eggs with the markings rather uniformly distributed were usually spotted only one color (Fig. 15, upper left and middle eggs); eggs with wreaths and caps tended to have a background (sometimes blurred) of many fine spots or a few large ones, all of light color; on this background were a few small, sharply defined darker marks.

Individual females' spot patterns and colors tended to be consistent; e.g. when eggs from 10 clutches were intermingled, one unfamiliar with the clutches could

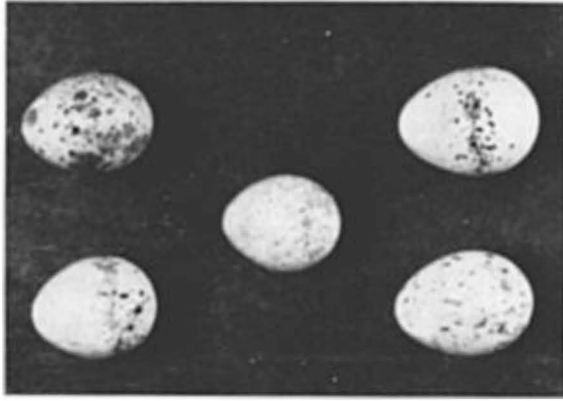


FIGURE 15. Representative markings of Prairie Warbler eggs. These eggs show approximately the full range of spotting observed, from least to most; faint pencil lines are observable on some of them. (Photograph by Raymond Schneider.)

usually reassemble them correctly. An occasional female produced eggs that varied.

The final egg of the clutch tended to be slightly differently marked (compare Mousley 1917, Nice 1937: 111–112); in about 50% of clutches it could be accurately identified by selecting the egg least like the others. No tendency was evident for the difference to involve more or less spotting, darker or lighter pigment, etc.

Shape.—Shapes varied considerably; five were common: oval, pyriform, long oval, long pyriform, short oval. Of these, the first two probably were most frequent. Bent (1953: 432) states that “eggs vary in shape from ovate to short ovate, with occasionally a tendency toward elongate-ovate.” Elongation (length/breadth) is analyzed statistically below.

MEASURABLE CHARACTERISTICS

All measurable characteristics, including weights, are referred to as “measurements”; 333 eggs laid by 82 females provided the data. Lengths and breadths were measured with vernier calipers.

Frank W. Preston (pers. comm.) wrote, “I would regard . . . volume as the best single specification of size” and informed me that approximate volume could be calculated from length and breadth “on the assumption that the egg does not differ much from a prolate ellipsoid of circular cross-section (at right angles to the long axis). The formula is $V = 0.524 B^2 \cdot L$, where B is breadth, L is length, and 0.524 is $\pi/6$. There will be a slight error because your measured B is maximum diameter, not diameter at the middle of the length, and because most birds have a slight ‘negative bicone.’ Neither error is large . . . and you could find the amount [by determining the volume of water displaced by eggs of Prairie Warblers and modifying the formula accordingly].” To correct the error referred to, I determined the actual volume of 37 Prairie Warbler eggs. David Porter kindly suggested that I use a small beaker whose top was ground smooth. When this apparatus was completely filled with distilled water to produce a

TABLE 59
MEASURABLE CHARACTERISTICS OF ALL EGGS¹

	Length	Breadth	Volume	Elongation	Weight	Density
N	333	333	333	333	40	39
Mean	15.95	12.33	1.211	1.29	1.299	1.08
Maximum	17.7	13.3	1.48	1.45	1.50	1.11
Minimum	14.3	11.3	0.91	1.14	1.10	1.04
SD	0.68	0.38	0.105	0.05	0.09	0.02
C ²	0.042	0.030	0.087	0.042	0.072	0.014

¹ Methods and terms are discussed on pages 177–178. Measurements are in mm; volume is in ml; elongation is length over breadth; weight is in g; density is weight over volume.

² C is the coefficient of variation.

meniscus and a ground glass plate was laid on the meniscus, all visible air could be excluded and a tight seal formed. I then weighed separately the egg, the apparatus filled with water, and the apparatus filled with water and the egg; calculated the weight of displaced water by subtraction; and converted weight to volume. A convenient feature of this method is that eggs can be used although they have become lighter than water; since air is excluded, floating eggs are fully submerged by pressure of the ground glass plate. Measured volumes indicated that a more suitable coefficient in Preston's formula is 0.499 (mean of 37 cases; SD 0.018, extremes 0.528 and 0.425). Unless specifically stated, no distinction is made between eggs whose volumes were calculated and those whose volumes I measured.

Elongation is length over breadth.

Only weights taken on the day an egg was laid were considered, unless otherwise specified. An analytical balance accurate to 1 mg was used, but weights are rounded to the nearest cg. Density was determined by dividing weight by volume.

Table 59 summarizes statistics for all measurements, without analysis of factors associated with variation. The least variable characteristic was density; volume and weight had the greatest relative variation. Preston (pers. comm.) has found that breadth nearly always varies less than length in avian eggs.

Eggs showing extreme lengths and breadths measured 17.7×12.6 ; 14.3×12.5 and 14.3×11.3 ; 16.0×13.3 ; 14.8×11.3 ; 15.1×11.3 ; and 14.3×11.3 mm. The measurements of the most elongated egg were 17.1×11.8 mm.

Variation according to sequence of egg in clutch.—Eggs may have become broader and their volume greater as laying of the clutch progressed, as the data in Table 60 suggest. In analyses of variance of both breadth and volume (shown in Table 60), $P < 0.01$. Student-Newman-Keuls tests of mean volumes show significant ($P < 0.05$) differences between egg 5 and each of the other eggs; the difference in the means of egg 1 and egg 4 are close to significance. In breadth, eggs 1, 2, and 3 differ from egg 5; the difference between eggs 4 and 5 approaches significance. None of the other parameters varied according to egg number (the sample of weights is obviously inadequate); but it is suggestive that mean length increased steadily although nonsignificantly from eggs 1 through 5.

If it may be assumed that within the individual clutch eggs with greater volumes produced larger young at the time of hatching (see Schifferli 1973), then the tendency for the later eggs of the clutch to be larger might have the following

TABLE 60
MEASURABLE CHARACTERISTICS OF EGGS, ACCORDING TO ORDER IN WHICH LAID¹

	Egg 1	Egg 2	Egg 3	Egg 4	Egg 5
Length					
N	83	70	71	47	5
Mean	15.82	15.92	16.02	16.06	16.62
Extremes	17.7-14.3	17.6-14.3	17.6-14.8	17.4-14.5	17.0-16.3
SD	0.76	0.66	0.64	0.62	0.35
Breadth					
N	83	70	71	47	5
Mean	12.27	12.31	12.36	12.39	12.70
Extremes	13.1-11.3	13.0-11.3	13.1-11.5	13.3-11.6	12.9-12.3
SD	0.37	0.35	0.33	0.42	0.25
Volume					
N	83	70	71	47	5
Mean	1.190	1.204	1.223	1.231	1.336
Extremes	1.42-0.95	1.48-0.91	1.45-0.98	1.41-0.97	1.37-1.28
SD	0.10	0.10	0.10	0.11	0.04
Elongation					
N	83	70	71	47	5
Mean	1.29	1.30	1.30	1.30	1.31
Extremes	1.45-1.14	1.44-1.18	1.43-1.21	1.41-1.14	1.39-1.26
SD	0.07	0.06	0.05	0.05	0.05
Weight					
N	11	11	10	8	0
Mean	1.261	1.306	1.341	1.290	—
Extremes	1.32-1.15	1.41-1.24	1.49-1.10	1.50-1.12	—
SD	0.07	0.06	0.10	0.13	—
Density					
N	11	10	10	8	0
Mean	1.08	1.09	1.09	1.08	—
Extremes	1.10-1.05	1.10-1.06	1.11-1.06	1.11-1.04	—
SD	0.02	0.01	0.02	0.02	—

Selected analyses of variance

Source	df	Sum of squares	Mean square
Length			
Main effect	4	10.329	2.582
Error	271	370.091	1.361
Total	275	380.420	
$F = 1.90, P > 0.05$			
Breadth			
Main effect	4	2.259	0.565
Error	271	35.724	0.132
Total	275	37.983	
$F = 4.28, P \approx 0.001$			
Volume			
Main effect	4	0.254	0.063
Error	271	2.627	0.010
Total	275	2.881	
$F = 6.30, P < 0.001$			

¹ Any egg whose sequence in its clutch is known is included, regardless of clutch size and whether data for other eggs in the clutch are lacking. Length and breadth are in mm; volume is in ml; elongation is length over breadth; weight is in g; density is weight over volume.

adaptive significance: The putative larger size of the newly emerged nestling might help compensate for its later hatching (Chapter 23), i.e. for any advantage possessed by young of earlier eggs as the result of getting an earlier start on post-embryonic life. However, the tendency for eggs to be larger as sequence number advanced was not uniform; eggs of some females increased in length or breadth while the other dimension decreased.

For individual clutches, extreme examples of change between first and final eggs, which almost always represented the extremes in the clutch, were these: Length increased from 15.9 to 17.2 mm (18.1%) and decreased from 15.7 to 14.5 mm (7.6%). Breadth increased from 12.5 to 13.1 mm (4.8%) and decreased from 12.3 to 11.9 mm (3.3%). Volume increased from 1.18 to 1.38 ml (16.9%) and decreased from 1.09 to 0.97 ml (11.0%).

Variation according to clutch size.—No significant difference was found in egg measurements according to clutch size, but this may be attributable to the presence of so few five-egg clutches. Mean volume of 49 eggs from 3-egg clutches was 1.21 ml, and the figure for 200 eggs from 4-egg clutches was the same; 31 eggs from clutches of 5 had a mean volume of 1.25 ml. In an analysis of variance $F = 2.65$ ($df = 2$ and 277); $F_{.05} =$ about 3.03. The slightly greater volume of eggs in five-egg clutches arises from their being somewhat longer (mean = 16.3 mm) than other eggs. Since no differences were significant, extended discussion is unwarranted. However, I did consider whether, if larger samples should reveal that eggs in five-egg sets had greater volumes, this might be caused by the fact that only five-egg sets have a fifth egg. This question arises because, as shown above, egg 5 has a greater volume than all other eggs. But the explanation proved to be unlikely: egg 1 from 5-egg clutches was larger than egg 1 from 4- and 3-egg clutches, and the same was true of eggs 2 and 3. The differences were not significant; but the indication is that if eggs of five-egg sets prove to be larger when analyzed in sufficient numbers, the difference will not be confined to any particular egg in the set.

Variation according to clutch number and date.—It was impossible in my small sample to separate potential effects of increasing clutch number from effects of advancing date, and I tested the data only for variation according to clutch number. The significant differences found were these: Mean length of 159 eggs from first clutches was 16.04 mm (SD 0.67 mm); mean length of 143 eggs from replacement clutches of whatever number was 15.82 mm (SD 0.71 mm); $t = 2.77$; $df = 300$; $P < 0.01$. Mean elongations of the two samples were, respectively, 1.30 (SD 0.05) and 1.28 (SD 0.06); $t = 3.15$; $df = 300$; $P < 0.005$.

However, these differences probably were associated with the fact that replacement clutches contained fewer eggs than first clutches (see the relationship between clutch size and date, Chapter 18). Since mean egg length increased progressively (not significantly) from egg 1 through egg 5, the mean length of eggs from replacement (= later) clutches may have diminished somewhat, simply because there were fewer eggs 4 and 5 in those clutches. This suggestion is supported by a comparison of 102 eggs from 4-egg first clutches and 73 eggs from 4-egg second clutches. With clutch size thus held constant, differences between means of all parameters were nonsignificant.

Variation according to age.—Females older than 1 year laid eggs of greater

TABLE 61
MEASURABLE CHARACTERISTICS OF EGGS,¹ ACCORDING TO AGE OF FEMALE

	Old females	Yearlings
Length		
N	135	69
Mean	16.04	15.90
Extremes	12.6-14.5	17.7-14.3
SD	0.65	0.62
Breadth		
N	135	69
Mean	12.37	12.21
Extremes	13.2-11.3	13.3-11.3
SD	0.32	0.44
Volume		
N	135	69
Mean	1.228	1.184
Extremes	1.44-0.96	1.41-0.91
SD	0.088	0.118
Elongation		
N	135	69
Mean	1.30	1.30
Extremes	1.45-1.18	1.40-1.18
SD	0.06	0.05
Weight		
N	32	7
Mean	1.318	1.223
Extremes	1.50-1.15	1.32-1.10
SD	0.084	0.100
Density		
N	31	7
Mean	1.09	1.08
Extremes	1.11-1.06	1.10-1.05
SD	0.01	0.02
Tests of significance		
Length	$t = 1.48$; $df = 202$; $0.20 > P > 0.10$.	
Breadth	$t = 2.96$; $df = 202$; $0.005 > P > 0.001$.	
Volume	$t = 3.00$; $df = 202$; $0.005 > P > 0.001$.	
Elongation	$t = 0.55$; $df = 202$; $P > 0.50$.	
Weight	$t = 2.62$; $df = 37$; $0.025 > P > 0.01$.	
Density	$t = 1.95$; $df = 36$; $0.10 > P > 0.05$.	

¹Length and breadth are in mm; volume is in ml; elongation is length over breadth; weight is in g; density is weight over volume.

average breadth, volume, and weight than did yearlings, as data and results of t tests in Table 61 reveal. Length, however, did not vary significantly with age (compare Nice 1937: 114-116). Eggs of older birds averaged 1.3% broader, 3.8% larger in volume, and 7.8% heavier than eggs of young females.

To test whether the larger size of eggs of old females might be a function of the possibility that they lay larger clutches (Chapter 18), I compared volumes of 76 eggs from 4-egg clutches of old females with volumes of 47 eggs from 4-egg clutches of yearlings. The mean for old birds was 1.23 ml (SD 0.10 ml), for yearlings 1.18 ml (SD 0.13 ml); $t = 2.40$; $df = 121$; $0.025 > P > 0.01$. It is therefore unlikely that the size differences between eggs of the two age classes was associated with any difference in clutch size.

TABLE 62
SOME MEASUREMENTS OF EGGS OF SELECTED FEMALES¹

	Female A	Female B	Female C	Female D	Female E	Female F
Length²						
N	9	7	9	24	7	8
Mean	16.3	15.2	16.1	16.1	15.1	15.8
Extremes	16.0-16.8	15.0-15.4	15.1-17.0	14.5-16.0	14.5-15.7	15.1-16.4
SD	0.27	0.15	0.58	0.33	0.35	0.44
C	0.017	0.010	0.436	0.021	0.023	0.028
Breadth³						
Mean	12.4	12.3	11.8	12.4	11.6	12.2
Extremes	12.1-12.6	12.1-12.4	11.3-12.3	12.0-12.8	11.5-11.8	12.0-12.5
SD	0.16	0.11	0.34	0.23	0.11	0.17
C	0.013	0.009	0.029	0.019	0.010	0.014
Volume⁴						
Mean	1.25	1.14	1.12	1.19	1.02	1.18
Extremes	1.18-1.33	1.11-1.17	0.96-1.28	1.06-1.25	0.97-1.09	1.09-1.28
SD	0.05	0.03	0.10	0.05	0.04	0.07
C	0.040	0.026	0.089	0.042	0.039	0.059
Elongation⁵						
Mean	1.32	1.24	1.37	1.24	1.29	1.30
Extremes	1.30-1.33	1.22-1.26	1.34-1.41	1.18-1.28	1.25-1.33	1.25-1.34
SD	0.01	0.01	0.03	0.03	0.03	0.03
C	0.008	0.008	0.022	0.024	0.023	0.023

¹ All females at least 2 years old that supplied data from at least 2 clutches are indicated. Length and breadth are in mm; volume is in ml; elongation is length over breadth; C is the coefficient of variation.

² $F = 17.54$; $df = 5$ and 58 ; $P < 0.01$.

³ $F = 21.31$; $df = 5$ and 58 ; $P < 0.01$.

⁴ $F = 14.77$; $df = 5$ and 58 ; $P < 0.01$.

⁵ $F = 36.06$; $df = 5$ and 58 ; $P < 0.01$.

Individual differences.—Lengths, breadths, volumes, and elongations of eggs of six old females for which I had measurements from at least two full clutches are presented in Table 62, as are values of F in analyses of variance ($df = 5$ and 58). All F 's are significant far beyond the 0.01 point. Interesting in addition to this evidence of individuality is the considerable variation in the eggs of female C and the small variation in those of female B.

Weights of full sets.—Each egg of four clutches was weighed on the day it was laid. (1) A second clutch of four eggs laid in May by an old female weighed 5.67 g. Each egg was heavier than the preceding; extremes were 1.32 and 1.50 g. (2) A set of three eggs laid in July by an old female whose previous history was unknown weighed 3.84 g. The eggs grew progressively heavier, from 1.19 to 1.36 g. (3) The second clutch laid in the following year (May) by the old female referred to just above consisted of four eggs and weighed 5.37 g. Egg 1 was heaviest, egg 3 lightest, egg 4 next to heaviest. Extremes were 1.37 and 1.33 g. (4) A clutch of three eggs laid in July by an old female whose previous history was unknown weighed 4.13 g. Weights increased progressively from 1.31 to 1.49 g.

Using mean weights of single eggs in 3-, 4-, and 5-egg clutches (means not shown because not significantly different), I calculated mean weights of full clutches as follows: 3 eggs, 3.96 g; 4 eggs, 5.15 g; 5 eggs, 7.00 g.

Egg weights in relation to female weights.—The mean weight of 41 females caught during the breeding season was 7.74 g (pp. 544-545). Actual weights of the 2 four-egg clutches referred to above amount to 73% and 69% of this mean

body weight; actual weights of the 2 three-egg clutches constitute 50% and 53% of the mean body weight. Calculated weights given in the preceding paragraph are 51% (3 eggs), 67% (4 eggs), and 90% (5 eggs) of the mean body weight.

The mean weight of all 40 eggs weighed, 1.30 g, was 16.8% of female mean body weight during the breeding season; the lightest egg (1.10 g) was 14% and the heaviest egg (1.50 g) 19% of mean female weight.

A female that I caught just after she had gone to the nest to roost at 2000, about 9.5 hours before she laid the last (fourth) egg of a second clutch, weighed 11.7 g.

Loss of weight by eggs.—Fresh eggs left uncovered at air temperature all night in the laboratory lost about 3 mg in 12–15 hr, i.e. 0.2% of mean egg weight.

Only one weighed clutch survived predation long enough to provide information on weight loss during the incubation period. The eggs from that set were weighed on 8, 9, and 10 July, each on the day it was laid. Weights were also obtained about 133 hours after the last egg had been laid, i.e. some halfway through the incubation period, and again about 115 hours later, i.e. 12–24 hours before hatching. Weights per egg at these three times are given in chronological order, with percentages of weight loss since laying also shown: egg 1—1.19 g, 1.12 g (6%), 1.05 g (12.4%); egg 2—1.29 g, 1.20 g (6.9%), 1.13 g (12.2%); egg 3—1.36 g, 1.27 g (6.5%), 1.18 g (13.1%) (compare Schrantz 1943: 376).

Densities of these eggs at the three weighings were as follows, with percentage of reduction since last weighing also shown: egg 1—1.10, 1.03 (6.4%), 0.97 (11.8%); egg 2—1.10, 1.03 (6.4%), 0.97 (11.8%); egg 3—1.09, 1.02 (6.4%), 0.94 (13.8%).

Variation in eggs of individual female.—For one female older than 2 years, I obtained weights of 16 eggs from 8 clutches laid during two summers. The mean was 1.289 g (SD 0.067 g); extremes were 1.37 and 1.15 g. The heaviest egg was 19% heavier than the lightest.

CHAPTER 20

THE TIMING OF LAYING; BEHAVIOR; THE INCUBATION PATCH

BEGINNING OF LAYING

Dates.—This section analyzes dates on which 159 females laid egg 1 in first nests, 1952–1966. Individuals present in more than 1 year are counted each time they supplied data. Omitted are cases in which predators, cowbirds, or I probably caused females to abandon nests, postponing laying.

Table 63 presents dates on which egg 1 was laid by the female that laid earliest each year, the female that laid latest but at the beginning of the season (defined on p. 89) in the 14 years for which I obtained this information, and the middle approximately 66% of all females in years in which at least seven were under observation. The table also shows the number of days (inclusive) between beginning of laying by the females that laid earliest and latest, referred to as the “egg-1 interval.” Finally, it presents the duration of the interval in which the middle 66% of females began to lay in 7 years.

Extreme earliest annual egg 1 dates were 2 May and 15 May; the mean earliest date for 15 years was about 8 May. The mean of 14 annual mean dates was about 14 May. Extreme latest egg 1 dates were 12 May and 29 May; the mean for 12 years with at least six cases was about 23 May. The egg-1 interval varied from 8 to 23 days; its mean length was about 16 days. The length of the interval in which the middle 66% of females began to lay ranged from 4 to 16 days; the mean of 9 intervals was 9 days. (In 1964, 9 of 15 females being studied laid egg 1 in a 4-day span, an unusual example of synchrony.) No correlation appeared between the date on which the earliest female laid and the duration of the egg-1 interval; but data from a long period might reveal a negative correlation.

Duration of final phase of growth of egg.—Before turning to possible effects of weather, the duration of the interval between the sudden acceleration of growth of the ovum (Romanoff and Romanoff 1949: 203–205) and its laying will be considered. If it can be assumed that the period of rapid growth varied little in normal circumstances (ideal weather, female in reproductive condition), then its approximate maximum duration can be inferred from the usual time between nest failure and laying of egg 1 in the replacement nest, which should about equal the maximum time required for the final maturation (compare Nice 1937: 102, 111; Kluijver 1951: 48). Most frequently the interval between nest failure and start of laying in the next nest was about 115 hours; thus, many females lost a nest on day 1, began to rebuild next day, finished active building on day 4, had a 1-day inactive phase, and laid on day 6 at about 0540 (see below). I therefore assume that the ovum destined to be egg 1 normally began final rapid maturation a little less than 5 days before it was laid. If ovulation occurred about 24 hours before laying (Romanoff and Romanoff 1949: 214), the final growth phase in the follicle was about 4 days long.

The numerous instances in which egg 1 was laid considerably more than 5 days

TABLE 63
DATES OF THE LAYING OF EGG 1,¹ 1952-1966

Year	Number of females	Earliest date	Latest date	Mean date	Egg 1 interval ²	Period of laying egg 1 by middle 66% of females	
						Date	Duration in days
1952	10	6/5	24/5	14/5	19	7/5-19/5	13
1953	10	10/5	29/5	18/5	20	14/5-23/5	10
1954	9	2/5	20/5	11/5	19	7/5-15/5	9
1955	4	7/5	21/5	15/5	15	—	—
1956	2	14/5	—	—	—	—	—
1957	7	2/5	20/5	10/5	19	4/5-15/5	12
1958	21	12/5	25/5	17/5	14	13/5-19/5	7
1959	17	6/5	21/5	12/5	16	9/5-17/5	9
1960	16	3/5	25/5	17/5	23	7/5-22/5	16
1961	16	13/5	29/5	20/5	17	18/5-22/5	5
1962	11	9/5	29/5	14/5	21	10/5-18/5	9
1963	11	6/5	18/5	12/5	13	10/5-14/5	5
1964	15	4/5	12/5	8/5	9	7/5-10/5	4
1965	5	8/5	16/5	11/5	9	—	—
1966	6	15/5	22/5	19/5	8	—	—

¹ All dates are those on which females laid egg 1 in the first clutch of the season, excluding cases in which interference (e.g. predation) postponed laying.

² The egg-1 interval began on the day the earliest female laid egg 1 and ran through the day the latest female laid egg 1.

after nest building began are of special interest. In many of these the female probably started to build before final maturation had begun, and in others maturation may have been arrested or retarded. Such cases were most numerous at the beginning of the breeding season, when variation in the stage of the acceleration phase (Marshall 1961: 309-316) attained by females probably was considerable. However, external environmental conditions apparently were also capable of exerting important effects, as will be shown.

Effects of weather on laying of egg 1.—Evidence of effects of bad weather is episodic rather than statistical. Only 16 nests among more than 700 studied were completed but never laid in; 10 of these were concentrated into two brief periods associated with unusually severe weather. Each period and the behavior of females during it are described.

Period 1: In 1960, six females began to build on 2-3 May; four completed active building on 6 May, one on 7 May; one was still building on 7 May. Maximum daily temperatures on 2-6 May were never below 21.1°C, only twice below 24.4°C; no rain fell 2-5 May. Thus, five of the six females completed nests during normal or excellent weather. On 7 May prolonged cool weather began (published records erroneously report 8 May); from 8 May to 13 May daily highs were 11.7°, 11.1°, 5.6°, 8.3°, 13.3°, and 17.8°C. Rainfall during 6-10 May was 35.2 mm. Cool temperatures ended 14 May (high 25.0°C). Four of the females abandoned their completed nests without laying and began to build new nests when the weather improved (three laid egg 1 on 19 May, one on 21 May). The female whose nest was still incomplete on 7 May quit building for 4 days, then finished the nest but abandoned it and built another (laying 22 May). Thus only one of the six nests was used; egg 1 was laid in it on 15 May, i.e. after the rise in temperature and 8 days after active building ended; this was by far the longest observed inactive phase (Table 49).

Two other instances of failure to lay in complete nests followed the bad weather just described and may have been affected by it. Two females began replacement nests (after predation) on 14 May, when the temperature rose, finishing on 16 May; but they abandoned these and built again (one laying on 27 May, one on an unknown date).

Given the normal 1- to 3-day inactive phase of early May (Table 49) and the inference that the start of rapid growth of the ovum usually preceded egg laying by about 5 days, it is highly probable that some of the six females that began to build on 2-3 May had already entered the period of rapid growth of egg 1 when their nests were completed. If so, these eggs probably were either resorbed or were retained until laying began on 19 May and 22 May; had the eggs been dumped, the nests would very likely have been used for this (pp. 100-101).

The one female that did lay in a nest begun 2-3 May is especially interesting; she laid on 15 May, about 24 hours after warm weather resumed and 5 days after the coldest day of the cold spell. Therefore she probably ovulated almost immediately after improvement in the weather, suggesting that growth of the egg had been completed earlier and that ovulation was delayed. Romanoff and Romanoff (1949: 216) report that ovulation is the event in avian reproduction most easily affected by external and internal influences; Marshall (1961: 323) states that "[s]udden cold inhibits ovulation."

The average daily mean temperature for the 6-day cool period just discussed was 6.8°C. Another cool period, which occurred at the same stage of the breeding season but in 1954, is interesting to compare. From 4 May to 10 May 1954, maximum daily temperatures fluctuated between 11.7°C and 16.7°C; the average daily mean was 10.0°C. All of six females that had nests in which eggs were to be expected laid, although two had quite long building intervals. The 3.2° difference between mean temperatures of the periods in 1954 and 1960 may have had some part in this difference in female response, but 1954 also differed from 1960 in that 6 of the 7 days in 1954 were partly or entirely sunny.

Period 2: Five females finished building 11 May 1953; weather had been favorable during building. Heavy rain (81.4 mm) fell 12-19 May. Temperatures were nearly normal (Visher 1944: 476), except that 14 May was cool (high 10.0°C). Three females abandoned nests without laying, rebuilt, and laid 20, 22, and 24 May, respectively; two females did lay. In this same period, a sixth female abandoned a very advanced fragment; a seventh finished a nest on 12-13 May and laid 18 May after an unusually long inactive phase.

Except for these unusual episodes, I found no statistical relationship between long inactive phases and unfavorable weather, presumably both because samples were small and because factors (compare p. 154) other than weather probably affect the promptness with which females lay. Nor, with a possible exception to be described below, could I detect on the sixth and fifth days before laying of egg 1 in first nests (compare Kluijver 1951: 47-49) any patterns of air temperature that might have been associated with timing of laying. Temperatures on those days proved to be a random sample of Bloomington temperatures between 1 May and 25 May, suggesting that temperature was never low enough to inhibit the beginning of rapid growth of the ovum and/or that rapid growth

sometimes began more than 5–6 days before laying and was arrested. The evidence from 1960 (Period 1, above) that cold weather sometimes prevented laying makes the second alternative likely (compare Kluijver 1951: 48, Lack 1966: 6).

The possible exception referred to above was in 1964, when nine females laid egg 1 between 7 and 10 May; there had been a sharp rise in temperature on 2 May, and warm dry weather continued through 10 May.

Effect of weather on laying of eggs after egg 1.—Almost all evidence indicates that once egg 1 was laid weather had no effect on laying of the rest of the clutch (compare Kluijver 1951: 76). In the one possible exception, a female laid egg 1 in her second nest on 27 May; the temperature was -1.1°C that morning, and a severe frost killed much vegetation. The female did not lay on 28–29 May; these were normally warm, but the weather 5 days preceding each of these dates had been unseasonably cool (lows 3.9°C , means 10.0°C and 15.0°C). The female then laid egg 2 on 30 May; the temperature 5 days earlier had been warm. She did not lay again until 2 June, which was 6 days after the very cold morning on which egg 1 was laid; she also laid on 3 and 4 June. Weather may have produced these effects, but four somewhat similar cases (pp. 173–174) were not associated with low temperature.

Other weather effects.—Temperature as low as -1.1°C on the morning of laying did not affect laying, nor, normally, did heavy rain. In an exceptional case, violent storms between 2200 and 0500 (22–23 June 1960) almost certainly prevented female Prairie Warblers (as well as females of other species whose nests I was observing) from going to nests to lay. About 106 mm of rain fell; winds were violent and inflicted great damage on vegetation and property. Only one of four Prairie Warbler nests in which new eggs were expected on 22 June contained the expected egg; that egg was the only one that was the final egg of its clutch, and the female that laid it probably spent the night on the nest (see p. 192). In the nests that lacked expected eggs, laying resumed next day; clutch sizes were only 3, 2, 2 (compare Table 54), suggesting that the females had disposed of an egg wherever they happened to be on the morning of the storm.

The lowest mean temperature on a day preceding laying, i.e. the assumed day of ovulation, was 12.0°C , and the lowest minimum was 3.9°C .

Duration of pair-bonding period.—Hamilton (1961) proposed that the degree of sexual dimorphism in some pair-forming territorial species is “associated with conspecific mate location and selection (pair-formation), maintenance of pair-bond, and length of the pre-nesting ‘engagement’ period.” He believed that sexually dimorphic wood warblers have a “more rapid pair-bonding period” than monomorphic species (pers. comm.) and defined that period as the interval “between the initial pairing on the male’s territory and the date of laying of the first egg.”

To provide data that may be useful in testing Hamilton’s hypothesis, I determined 131 pair-bonding periods (in days, from pairing through the day preceding laying of egg 1) of Prairie Warblers that paired at the beginning of the season. Table 64 presents mean and extreme durations of all periods as well as of annual subsamples from 12 years in which I had at least four data. The mean of all periods was 12.6 days; extremes were 24 and 5 days.

For all 131 data and for annual subsamples no smaller than 6 I also analyzed

TABLE 64
DURATION IN DAYS OF PAIR-BONDING PERIODS,¹ POOLED AND ACCORDING
TO YEARS

	N	Mean	Extremes	SD
1952	6	11.2	16-8	3.1
1953	7	14.1	22-11	3.8
1954	8	13.9	20-9	4.8
1958	18	14.0	22-7	4.0
1959	16	10.1	20-7	3.4
1960	15	16.1	24-7	6.3
1961	14	14.3	23-10	3.9
1962	10	9.0	11-7	1.6
1963	11	11.2	22-6	5.0
1964	13	11.3	15-6	3.0
1965	4	10.5	15-5	4.1
1966	4	10.5	16-5	5.3
All years pooled ²	131	12.64	24-5	4.6

¹ The period began on the day a male paired and ended with the day before his mate laid egg 1. See text.

² The pooled data also include periods from 1956 and 1957.

the relation between duration of pair-bonding period and relative date of pairing (following the method described on p. 22). A negative correlation existed for the pooled data and for 8 of the 10 annual subsamples but was significant ($P < 0.05$) in only 3 years; it was not significant for the pooled data. Furthermore, two correlations were positive, one significantly. Regression of pair-bonding period on relative date of pair formation for the pooled data was almost significant ($t = 1.93$, $t_{.05} = 1.98$). But the regression coefficient was only -0.15 days per day of delay of pair formation; therefore early pair formation led to early laying (compare pp. 91-92 and 111-112).

Dates of first clutches elsewhere.—Selected earliest dates on which eggs have been reported elsewhere are shown below. Most authors speak of full sets; laying therefore began somewhat earlier than the dates reported: Florida—29 March (Florida race, A. H. Howell 1932: 409). Georgia—22 April (Burleigh 1958: 540). Alabama—27 April (Imhof 1962: 476). Virginia—first week of May (Jamison 1889, Daniel 1901). Kentucky—1 May (Mengel 1965: 418). Maryland-D.C.—14 May (Stewart and Robbins 1958: 298). New York—18 May (Bull 1964: 386). Massachusetts—28 May (Forbush 1929: 274). Michigan—27 May (Wood 1951: 405).

END OF LAYING

Latest dates on which clutches were begun in years in which my field work was adequate to discover last nests are shown below. All clutches consisted of three eggs; the last egg was laid each year 2 days later than the date shown. 1952—22 July; 1953—6 July; 1954—4 July; 1955—7 July; 1956—6 July; 1957—10 July; 1958—19 July; 1959—12 July; 1960—8 July; 1961—23 July; 1962—17 July; 1963—9 July; 1966—12 July.

The mean for 13 years was 12 July. Using this date and the annual mean date of earliest laying (8 May), the mean period between egg-1 dates in extremely early and extremely late nests each year was 66 days long.

Few late dates reported from other localities appear founded on sufficient observations, and many records refer to latest dates on which eggs (possibly well incubated) were found. Approximate laying dates in late nests follow: Kentucky—10 July (Mengel 1965: 418). Mississippi—10 July (inferred by me from the collection on 28 August of young still in juvenal plumage, by M. G. Vaiden pers. comm.). Georgia—5 August ("5 fresh eggs," Burleigh 1958: 540).

RATE OF LAYING

Unusually rapid rates.—Normally one egg was laid shortly after dawn on consecutive days. Of about 1100 occasions on which I visited nests to mark an expected egg, 2 new eggs were present instead of 1 in 3 instances. (1) A female of unknown age laid eggs 1 and 2 of her third clutch between 1530 on one day and 1020 on the next. (2) A yearling laid eggs 1 and 2 in her first nest between two inspections at about 1130 on successive days. (3) A female more than 1 year old laid eggs 2 and 3 in her first nest between an inspection at 0900 and another 26 hours later. In all 3 instances clutches of 4 eggs were deposited in 3 days.

In cases 2 and 3 the eggs may have been laid about 24 hours apart but at other than the usual time (about 0540). Of course, all three females laid at least one egg at an abnormal hour, if one discounts the possibility that the unexpected eggs were laid by individuals other than those to which the nests belonged. This possibility is extremely remote; all eggs in each nest looked approximately alike (see p. 176), and 4 is the modal clutch size.

Interrupted laying.—In only five cases was it clear that a female resumed laying in a nest after skipping one or more days. Details are presented in Chapter 18, because they seem more directly related to the subject of clutch size; see also Table 58.

In 10 nests in which I was marking each egg as laid, I found no change in the contents on a day when an egg was expected; next day a new egg was present. In 8 of these the number of eggs found was 3, in the remaining 2 instances, 4. Possibly one or more of these females skipped a day in laying; more likely a cowbird or predator removed an unmarked egg before my inspection. (Single marked eggs not infrequently disappeared during laying, with nothing to account for the disappearance.) As evidence of the rarity of skipping, on 58 mornings I went to nests to observe laying, and no bird failed to appear and lay on schedule.

HOURLY OF LAYING

The final egg of the clutch was usually laid later than the others; therefore that egg is discussed separately. The time the female went to the nest to lay is the "time of arrival," and the time she rose and apparently began to lay is the "time of laying." The period between arrival and departure is the "laying attentive period."

Eggs other than final egg.—Time of arrival to lay: Because of evidence (see below) of individuality in time of arrival, the sample of 33 cases is limited to one time per female. Almost all arrivals in the sample were to lay egg 2. The earliest was 0514, the latest 0547; the mean was 0528.8 (SD 8.2 min). Minutes elapsed be-

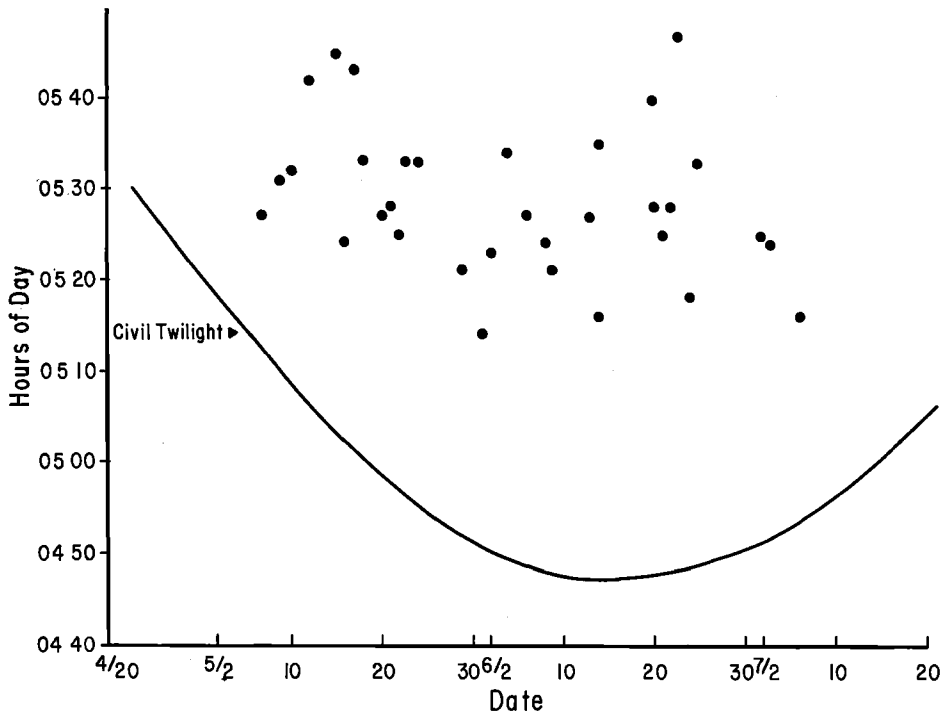


FIGURE 16. Time of arrival of females to lay on 33 mornings, 7 May–6 July, relative to time of civil twilight. Time is eastern standard. Each point represents a different female. The egg to be laid was not the final egg of the clutch; see text.

tween civil twilight and time of arrival numbered 14 in the shortest case, 59 in the longest; the mean was 34.4 min (SD 9.4 min). If it may be assumed that females awoke about when males did and that males began to sing shortly after awakening, then females usually arrived to lay 30–60 min after waking (see times of first songs, Figure 8).

Figure 16 plots the 33 times according to date and against the time of civil twilight. When time of arrival is regressed on date, the slope does not differ from 0 ($P \approx 0.10$). As a corollary, when minutes elapsed between morning civil twilight and time of arrival are regressed on date, the regression is significant ($= 0.770X$; $t = 2.48$; $df = 31$; $P < 0.025$). That is, although time of arrival did not change with advancing date, time of civil twilight did change. (The analysis was linear; few times were obtained after the summer solstice.) It appears, then, that time of arrival was determined by some mechanism not proximately linked to onset of twilight.

Interval between arrival and laying: In eight instances I could see well enough to determine when the female rose in the nest preparatory to laying. The intervals between time of arrival and rising were 9, 9, 9, 10, 10, 10, 12, and 15 min. The final three data were supplied by a single bird. In six additional cases, I hoop-netted females a few minutes after arrival to lay. Five caught 5, 5, 6, 6, and 8 min, respectively, after arrival had not yet laid.

TABLE 65
HOURS AT WHICH FIVE FEMALES WENT TO NEST TO LAY EGGS IN SAME
CLUTCH, EXCLUDING FINAL EGG

Female designation	Date	Sequence of egg in clutch	Time of arrival	Minutes on nest ²
A-56 ¹	14/5	1	0531	31
	15/5	2	0545	31
	16/5	3	0546	38
A-57 ¹	7/5	1	0527	16
	8/5	2	0541	26
	9/5	3	0543	28
B	15/5	1	0528	36
	16/5	2	0524	41
	17/5	3	0527	46
C	20/5	1	0520	35
	21/5	2	0528	28
	22/5	3	0528	—
D	1/6	2	0523	24
	2/6	3	0523	30
E	2/7	1	0529	36
	3/7	2	0524	44
	4/7	3	0521	54

¹ Female A was watched in both 1956 and 1957.

² In the text this time is referred to as the "laying attentive period."

These 14 instances indicate that most birds sat 9–15 min before laying. In subsequent calculations, I shall use 10 min as the interval between arrival and laying, and shall distinguish between calculated and observed times of laying.

Time of laying: Observations of rising and behaving as if laying, plus the case of the female that had laid when I caught her, provide these observed times: 9 May—0546; 17 May—0537; 18 May—0542; 20 May—0535; 14 June—0544; 20 June—0537; 2 July—0541; 3 July—0534; 4 July—0531. The last three were obtained from a single female.

When calculated times are pooled with these observed times, mean time of laying was 0538 in 35 cases.

Length of laying attentive period: Extreme lengths of 21 laying attentive periods were 16 and 54 min, the mean 32 min (SD 9.9 min); data were taken from 9 individuals. The bird that stayed only 16 min returned after 7 min and sat another 28 min. No other female returned in this way.

Evidence to be presented suggests that after laying females were in an exhausted or trance-like state for a time. The 7 females whose laying I observed remained on the nest for intervals of 13 to 44 min after they had begun to lay; the mean was 29 min (SD 10.0 min). For 15 females that I could not see well enough to know when laying began, 10 min can be subtracted from total lengths of the laying attentive periods. Thus calculated, these females stayed between 6 and 39 min after beginning to lay; the mean was 23 min.

Individuality in time of laying: Five females supplied more than one arrival time for a clutch; one of these was watched as she came to lay all eggs of her first clutch in 2 successive years. Table 65 presents times of arrival of these females, according to date and sequence of eggs in the clutch, and also shows lengths of laying attentive periods. The table suggests individual variation in hour of laying, as expected.

For example, female A arrived to lay egg 1 in 1957 four min earlier than on a comparable date in 1956; in each year, her times of arrival for eggs 2 and 3 were considerably later than those for egg 1 (compare the corresponding data for the other females); the difference between times for eggs 1 and 2 was identical in the 2 years. Several other instances of close similarity between a female's times on successive days are apparent. Individual differences in length of the laying attentive period are not clearly suggested. Some individuals may have tended to lay each egg a little later than its predecessor or predecessors (female A-56 and -57), while other birds may have tended to lay each egg a little earlier (female E).

Effect of weather: The foregoing discussion has assumed that weather conditions played no role. Most observations were made in good weather, but six made during rain gave no reason to believe that times or laying attentive periods were affected. Two females that I watched on rainy mornings I also observed 1 day earlier and later, respectively, on clear mornings; differences between their arrival times were only 4 min and 1 min.

Final egg.—Most females roosted on the nest the night before they laid the final egg, but a few did not. Time of laying probably was affected by this difference in behavior, producing greater variation in times for the final egg than for the others.

I inspected the nest when six females that had roosted on it left for the first time in the morning; the final egg was not yet present. Five of these females laid when they returned after the first inattentive period; the sixth laid when she returned from her second inattentive period. In two additional instances I refrained from going to the nest when the females left but judged from their behavior that they laid following the first inattentive period. The hour of leaving the nest for the first time varied between 0510 and 0545 in the 8 cases; the mean was 0529.

Times of laying in the 6 certain cases are shown below; in 5 the female's behavior was observed and 1 time (marked *) is calculated. 10 May—0607; 28 May—0543; 3 June—0545; 4 June—0550*; 22 June—0613; 30 June—0602. In addition, a female that had been frightened from her nest by a cowbird at 0508, on 26 May, returned and laid at 0605.

For three females, time of laying the final egg can be compared to time of laying one or more earlier eggs in the same clutch: Female A-57 (Table 65) laid eggs 1 and 2 at calculated 0537 and 0551, egg 3 at observed 0538, the final egg at observed 0607. Female D laid her final egg at 0545 on 3 June; she had laid the two immediately preceding eggs at calculated 0535. A female that laid her final egg at 0613 on 22 June had laid the preceding morning at 0535 calculated. Thus, these final eggs were laid 9–38 min later than their predecessors.

Four females that did not spend the night on the nest arrived to lay at the following times: 18 May—0523; 18 May—0545; 23 May—0533; 5 July—0534. Laying behavior was observed at 0543 by the female listed last. Calculated laying times for the others are 0533, 0555, and 0543, respectively. Comparison of these times with those for females that on similar dates had spent the preceding night on the nest suggests that the final egg was laid a little earlier if the female had not roosted on the nest. In fact, females that roosted off the nest showed no distinct tendency to lay the final egg later than its predecessors, as the following shows: Female B (Table 65) laid her eggs, in chronological order, at cal-

culated 0538, 0534, 0537, and 0533. Female C laid eggs 1, 2, and 4 at calculated 0530, 0538, and 0543. Female E laid at observed 0541, 0534, 0531, and 0543. Perhaps laying was accelerated by activity; females that spent the night on the nest remained there until a mean 0529 and presumably were less active just after dawn than were females that roosted off the nest.

Walkinshaw (1959) reports one time of laying as between 0500 and 0615 (Eastern Standard Time) in Michigan, and Daniel (1901) found that eggs were laid early in the morning in Virginia.

BEHAVIOR DURING LAYING

Once I caught a female shortly after she had arrived to lay. Noticing that her vent was dilating, I released her gently in my hand, where she remained and laid. Three of five efforts to repeat this were successful. Behavior on these occasions will be described separately from 11 observations during normal laying in nests. Visibility of the 11 nests varied greatly, and many details were seen only one or two times.

Situation and behavior preceding laying in hand.—Four females were held in one cupped hand with no constraint; one flew away without laying. Two were held in both hands, loosely confined. The egg had reached the vent in five of the six females and was clearly visible through the skin; in one female (held 57 min, released before she laid) the egg was less visible and appeared not to have reached the end of the cloaca.

As laying began, the birds raised the foreparts; the heels were bent, feet thrust forward; much of the weight rested on the heels and tarsometatarsi. The body was almost upright, tail projecting backward horizontally and supporting some of the weight. One female clutched tightly at the skin of my hand; possibly the feet grip the nest lining during normal laying. Two females elevated the foreparts and leaned sideways in my cupped hand; when the upper hand was removed after one of these had laid, withdrawal of support caused her to roll slowly sideward and lie almost on her side.

About 30 sec before the egg emerged females began to strain rhythmically; the anterior part of the body moved slightly forward and possibly upward every 2–3 sec; one bird sometimes also made one to three straining movements in rapid succession. Accompanying the straining of the body, the vent began to open; in each interval of relaxation, it closed somewhat; the next tensing resulted in a larger opening, so that dilation was progressively greater. One female seemed to make only 5 straining movements before the egg emerged; others made 10–15 such movements. The body feathers were erected (puffed) during the straining just described. One bird opened the bill slightly at or just before the end of each strain. (The female that I released after 57 min and before she laid sometimes opened and closed the bill slightly about twice per second as she breathed; she closed her eyes part of the time.) One female closed her eyes at the moment of laying; breathing seemed heavy; these details were not observed in others but perhaps were overlooked.

Laying in hand.—Females laid 13, 13, 16, and 18 min, respectively, after arrival at the nest and (in the same order) 7, 8, 10, and 10 min after capture.

Between capture and laying they had been removed from a hoop net (which took 1–2 min), banded, and examined for the presence of an incubation patch. These data were then recorded and the birds placed in position to lay, which they did promptly. In two cases I could see the egg emerge, rapidly, small end first (compare Weidmann 1964). It popped out when the vent dilated sufficiently; the shell was moist.

(Only one egg among all examined during the study had the pigment distributed around its small end, suggesting it may have turned in the uterus and lain in reverse-of-normal position.)

Behavior after laying in hand.—The condition immediately after laying appeared trance-like, as suggested by tipping sideways when unsupported (see above). The female that stuck her nail into my skin did not react when I disengaged it. Three sat in my hand about 5 min after laying and probably would have remained longer but biting insects caused me to move. (All four eggs were placed in the nests of the females that laid them; all females laid full clutches and incubated.)

Discussion.—Romanoff and Romanoff (1949: 232) say of the domestic fowl that the “vagina seems to be under the voluntary control of the hen” and that “[e]ggs may be retained for considerable periods if conditions for laying are unfavorable.” Weidmann (1964: 421) asserts that “[a]n egg that is ready for laying can be held back,” citing as evidence that parasitic cuckoos can postpone laying until the host has left the nest. I suggest that parasitic cuckoos, if not chickens, may be atypical. Prairie Warblers evidently had no voluntary control of laying, and inability to retain the egg was not limited to females caught at the moment of preparing to lay. I netted a female when she went to the nest at 1930 on the evening before her final egg was expected; she laid on the cage floor at the usual time next morning. Common Grackles and Mourning Doves have often entered my corn-baited traps and laid during the brief periods before I removed them (compare Weller 1959: 342).

Behavior preliminary to laying in nest.—Females went silently to the nest and entered immediately. Flight to the nest usually was long and direct, birds appearing without warning on or near the rim. One female repeatedly changed position in the nest for 2 min, then settled down in preparation to lay. Another appeared to doze for 2 min. Several rose to look beneath them.

Laying in nest.—Shortly before what appeared to be laying, every female rose, held the head and foreparts high, the breast drawn back from the nest wall. The region of the vent was deep in the nest, tail cocked upward at 30–45° above horizontal. After 1–3 min, the posterior part of the body sometimes rose slowly so that the line of back and tail were approximately horizontal. Most of the body was visible after this rise; the position looked less tense than before, and the impression was that the egg had been laid. Durations of the period in which the foreparts were held high, regardless of whether the posterior was depressed or raised, were 3–7 min; the mean of seven cases was 5 min.

On one to several occasions I observed opening and closing of the bill repeatedly for up to 4 min and rhythmic movement of the back and tip of the tail, possibly associated with breathing but more likely with the muscular contractions observed in the birds that laid in my hand. One female called Chek

five or six times during the period of laying; I was 2 m away and she had taken no previous overt notice of me. (Except in cases of the captured birds, I was probably not close enough to hear very soft vocalizations.)

Behavior after laying in nest.—After standing high in the nest, females settled deeply into it in the incubating position, sometimes after first looking beneath them and/or probing with the bill.

Male behavior during laying in nest.—With one exception, males never escorted females to the nest or visited the nest during laying. Most sang elsewhere on the territory. In the exceptional case a male accompanied a female to within 10 m of the nest and remained in or near the nest tree for 12 min, five times going to the nest and looking at the female. During the 4 min in which she rose and laid, the male was at the nest twice and called Seep once. He then left but in 3 min returned and passed food to the female, which she ate. He left again for 5 min but returned, and the female again appeared to receive something from him.

DEVELOPMENT OF INCUBATION PATCH

Unless the contrary is stated, references to development of the incubation patch involve only defeatherization, and nests mentioned were the females' first of the season. The patch probably usually began to lose its feathers about 3 days before the laying of egg 1. Since the mean interval between the end of active building and the laying of egg 1 in first nests was about 2.5 days (Table 49), ordinarily the patch began to develop just at the end of active building; but observations to be described suggest that development was only indirectly related to the timing of building (see Bailey 1952).

Females examined before laying.—None of seven birds caught 1–2 days before they began to build had incubation patches, nor had 4 additional females caught during active building (one on day 1, two day 3, one on day 5).

I interfered as follows with one of the birds that on day 3 of building had had no patch: When she finished her first nest, on 7 May, I took it. She began to rebuild next day, and I removed the nest the afternoon of 11 May, the day it was finished. Probably egg 1 would not have been laid next day; i.e. it is unlikely that the female had ovulated or did ovulate. She started a third nest on 12 May, and I caught her on 13 May. A bare patch was present but possibly not of full width. The episode suggests that the incubation patch will lose feathers even if external events prevent ovulation and laying, as my intervention probably had.

Females examined after beginning of laying.—I caught six females when they went to their nests to lay. Three netted on the day they laid egg 1 had patches whose skin did not look as vascularized and as loose as the skin of fully developed incubation patches and retained a few scattered down feathers. The patch of one appeared narrower than it would ultimately be, suggesting that the last contour feathers to be lost are at the margins.

Patches of three females caught on the day they laid egg 2 were full size and looked like those just described, except that one retained no down feathers on it. One of the three had begun to build on 13 May and finished on 17 May; she

had waited 5 more days before laying egg 1. Her patch on 24 May appeared no more completely developed than was that of a female (also caught when she laid egg 2) that had begun to build only 8 days before capture, suggesting that development of the patch was related to changes associated with growth and laying of the eggs rather than to completing of the nest (see Lehrman 1961: 1287–1289).

Females examined during incubation.—All of about 30 females caught 1–2 days after completing the first clutch had fully developed patches.

OTHER RELATED BEHAVIOR

Relations between pair on days of laying.—During all days on which eggs were laid except the last day (when full-scale incubation began), the pair spent much time together, the male usually following the female (sometimes only 3–5 m from her). Crouching and other evidence of tension was unusual and was observed only when he approached within 10–20 cm of his mate. Copulation, attempted copulation, and solicitation were not seen.

Frequency of the male's song is shown in Tables 11 and 12. Often when the female was not near him, she called immediately following his songs (p. 69).

Beginning of incubation.—Probably every female spent part of each day of laying sitting on the nest. This behavior is dealt with in Chapter 21.

Introduction of nestling.—Once I put a Yellow-breasted Chat 50 hours old in the second nest of a female Prairie Warbler 3–4 min before she arrived to lay egg 2, on 10 June. Her first nest, which contained large nestlings, had failed on 2 June. At 0521, she went to the nest and after looking into it for 25 sec entered and sat. At 0605, presumably having laid, she rose, and backed out of the cavity; the chat gaped until the female sat again. She left at 0612 and at 0627 returned with food and delivered it to the chat; after perching on the rim for 2 min, she sat. At 0648, she left. When she did not return for 1 hour, I removed the chat to prevent chilling.

Emlen's (1941: 217) experience that the female Tricolored Blackbird "brought very little if any food to the nest until she had finished laying" has been mentioned on page 160. In that species "[i]ncubation behavior . . . usually starts with the laying of the last egg, or on the succeeding day" (Emlen *op. cit.*: 210). In contrast, female Prairie Warblers sat on the nest from time to time on the day on which they laid egg 1 (Chapter 21). Since incubating warblers regularly fed introduced nestlings (p. 231) and the tendency to incubate was already present during the laying interval, the feeding response to the introduced chat is not unexpected.

CHAPTER 21

INCUBATION AND THE TIMING OF ATTENTIVENESS IN FEMALES

Attentive behavior includes both incubating and standing over the eggs, shading them. Only the female performed these activities; a conflicting statement by Daniel (1901) is uncorroborated. Probably all females incubated at times before laying the final egg (compare Lehrman 1961: 1284–1286, Weeden 1966). Differences between my data on incubation during the laying interval and during the incubation period (defined p. 235) have caused me to analyze the data separately.

Nests are dated according to the date egg 1 was laid. The interval between the start of the female's first inattentive period of the day and the end of her last inattentive period is the "active day," in contrast to the "interval of night nest." Data on attentiveness during the active day were obtained by two methods.

Nest-inspection method.—When I inspected a nest I regularly recorded whether the female was present, the time, and other relevant matters (see Davis 1954), obtaining data from several hundred nests of over 200 females during 16 breeding seasons, at all daylight hours and in all weather.

Nest-watch method.—Individual nests were observed for long periods, usually from first light until nightfall. Four day-long watches were carried out before the laying of the final egg, i.e. before the incubation period began; 24 others, including 2 that lasted slightly less than 1 day, were conducted during the incubation period. Details relating to these incubation-period watches are presented in the next paragraph. Many short watches during the incubation period supplemented these longer observations.

Results of the 24 long watches in the incubation period are summarized in Table 66. The observations involved 10 females (1 of them in 2 successive years) and 12 nests. Two watches of less than full daylight interval (one from 0645 to darkness, the other from 0445 to 1445) are retained in the sample in order to increase the number of females whose behavior is analyzed. Further, one of these two was the only long observation during uninterrupted heavy rain; most other watches were carried out in generally fair weather, with occasional brief showers during some. Extremes of daily mean temperature were 12.2°C and 28.6°C; daily means were between 16.1°C and 23.9°C on 18 of the days.

Because of apparent individual differences among females, inequality in number of watches per individual would bias some calculations if all watches were considered. To avoid this result, a sample was selected in which each female is represented only once, by the first watch carried out at her nest following day 1 of her incubation period (unless, as happened twice, she was observed only on day 1). Cases in this sample are marked * in the first column of Table 66.

ATTENTIVENESS BEFORE INCUBATION PERIOD

Data from nest inspections.—Methods: Table 67 presents data from 882 nest inspections, distributed according to time of day, day of laying, and nest number in

TABLE 66
SUMMARIES OF 24 DAY-LONG¹ NEST WATCHES DURING THE INCUBATION PERIOD

	Active day length, min ²	Percent attentive ³	Attentive Periods				Inattentive Periods			
			N	Length			N	Length		
				Mean	Median	Extremes		Mean	Median	Extremes
Female 1										
17 May—day 1	844	64.0	15	33	34	47–18	16	22	19	48–11
*24 May—day 8	847	82.3	19	36	33	65–9	20	9	9	14–3
28 May—day 12 ⁴	849	72.2	23	25	27	35–2	24	11	9	28–3
28 May—day 1 ⁴	843	75.4	19	32	29	58–22	20	12	10	24–4
Female 2										
*18 May—day 1 ⁵	—	64.7	16	27	31	57–19	16	21	14	30–11
26 May—day 9 ¹	—	—	11	39	36	51–25	12	9	7	18–5
Female 3										
2 June—day 1	863	73.0	24	25	30	55–13	25	10	11	13–5
*9 June—day 8	842	83.6	16	43	40	68–30	17	9	8	17–5
30 June—day 1	864	82.3	18	39	36	68–18	19	10	8	15–5
7 July—day 8	841	81.8	15	46	41	123–20	16	11	12	19–4
Female 4										
3 June—day 1	882	66.6	22	26	27	40–13	23	14	10	61–4
*9 June—day 7	882	79.8	17	36	38	87–20	18	11	10	22–3
13 June—day 11	876	78.1	22	30	29	102–6	23	9	6	30–1
Female 5										
5 July—day 1 ⁵	—	67.4	11	56	52	67–41	11	21	22	29–17
8 July—day 4	856	74.9	12	51	53	64–9	13	19	17	34–6
*11 July—day 7	794	74.3	12	47	47	60–22	13	19	17	35–6
15 July—day 11	807	80.0	14	44	37	108–12	15	13	14	25–2
Female 6										
10 July—day 3	786	77.7	21	27	26	46–9	22	10	9	19–5
*14 July—day 7	796	78.5	18	33	30	63–12	19	11	10	20–4
18 July—day 11	720	80.7	14	43	33	72–29	15	12	13	20–6
Female 7										
*29 June—day 5	903	77.3	20	34	34	59–15	21	10	11	23–5
Female 8										
*22 June—day 10	715	77.8	9	56	46	117–23	10	21	22	31–11

TABLE 66 (Continued)

	Active day length, min ²	Percent attentive ³	Attentive Periods				Inattentive Periods			
			N	Length			N	Length		
				Mean	Median	Extremes		Mean	Median	Extremes
Female 9										
*7 June—day 7	846	79.6	19	34	33	73–11	20	10	8	35–6
Female 10										
*14 July—day 6 ¹	—	—	13	40	38	62–12	14	18	17	34–8
* Indicates 10 watches selected to provide one case per female; see page 197										

¹ Two watches were shorter; female 2's nest was watched on 26 May from 0445 to 1445, female 10's from 0645 until darkness.

² The active day is measured from the beginning of the first to the end of the last inattentive period.

³ Percentages are calculated for 960 min, 0430–2030.

⁴ These watches were carried out in successive years.

⁵ The female did not incubate on the night preceding the nest watch and came to the nest at about 0530.

the series built by the female in the particular breeding season; for this last, first nests are grouped in one subsample and all later nests in another. Only nests in which one or more eggs were laid were counted in numbering a female's nests. Attentiveness did not vary sharply from hour to hour, and the day is divided into only four intervals. The first began at 0600 (prior to which most females observed on the nest were probably laying, not incubating) and ended at 0830; the other three intervals began at 0830, 1230, and 1630. The intervals beginning at 0830 and 1230 lasted 4 hours, the final interval 3 hours. After 1930 on the day of laying the next-to-last egg, most females changed their behavior markedly (see p. 203); and use of 1930 as the end of the final interval is necessary to permit comparison of that day with other days of laying.

Data were tabulated (Table 67) and analyzed for days 1, 2, and 3 because nearly all were obtained at nests with 4-egg clutches. In the case of information from nests with 5-egg and 3-egg clutches, the day on which the next-to-last egg was laid was tabulated as day 3. Therefore, for sets of 5 eggs data from both days 2 and 3 of laying appear in Table 67 in the column "Day 2," and 3-egg clutches produced no data included under "Day 2."

Results; variation according to day of laying: The most obvious and consistent changes in attentiveness were correlated with advance of laying. With minor exceptions, attentiveness in each interval of days 2 and 3 was greater than it had been during the corresponding interval the day before. Nest inspections were distributed roughly evenly throughout the day on all days of laying, and percentages in Table 67 are probably fair estimates of daily attentiveness. Females were found on the nest on 20–30% of inspections on the day the next-to-last egg was laid, about three times as often as on day 1. Tested for independence, observations of attentiveness and inattentiveness per day at first nests differed significantly ($P < 0.005$); the same is true of data from later nests.

Results; variation according to time of day: Less evident in Table 67 is differential attentiveness according to time of day, but this variation probably was obscured by the day-by-day increase in attentiveness. Clearly, females were found on the nest more often before 1230 than after ($P < 0.025$). On day 1, after-

TABLE 67
ATTENTIVENESS¹ PRIOR TO LAYING OF FINAL EGG, ACCORDING TO HOUR
OF DAY, DAY OF LAYING, AND NUMBER OF NEST

Time and nest number	Day of laying ²							
	Day 1		Day 2		Day 3		Totals	
	Female on nest		Female on nest		Female on nest		Female on nest	
	N	%	N	%	N	%	N	%
0600-0830 ³								
First nests	5/36	14	6/35	17	7/29	24	18/100	18
Other nests	6/40	15	3/30	10	11/26	42	20/96	21
0830-1230								
First nests	3/55	5	10/64	16	12/39	31	25/158	16
Other nests	14/88	16	25/63	40	26/76	34	65/227	29
1230-1630								
First nests	3/47	6	1/32	3	3/31	10	7/110	6
Other nests	1/27	4	5/26	19	10/23	43	16/76	21
1630-1930 ³								
First nests	0/23	0	3/24	13	5/23	22	8/70	11
Other nests	0/13	0	0/16	0	2/16	13	2/45	4
Totals								
First nests	11/161	6.8	20/155	12.9	27/122	22.1		
Other nests	21/168	12.5	33/135	24.4	49/141	34.8		

¹ Attentiveness is measured by the nest inspection method (page 197). The denominator is the number of nest inspections, and the numerator is the number of times the female was found on the nest.

² Data from 3- and 5-egg clutches were tabulated as described on page 199.

³ Reasons for selecting 0600 and 1930 as terminal points for tabulation appear on page 199.

noon attentiveness was very slight; on subsequent days, particularly the day of laying the next-to-last egg, females often sat on the nest in the afternoon.

Results; variation between first and later nests; changes with date: In the first and last intervals of the day, females exhibited no consistently different patterns of attentiveness at first and later nests. Between 0830 and 1630, however, they were much less attentive at first than at later nests. A posteriori statistical comparison of the data selected from these hours is not permissible, but for purposes of further discussion it will be assumed that a difference existed. Possible explanations for this assumed greater attentiveness at later nests may be differences in states of females and external environmental differences associated with date. Environmental differences, if any, would probably involve food supply and feeding conditions. These possibilities will be explored.

This paragraph compares attentiveness at first and second nests from the same calendar period, 16 May-31 May. Distribution of inspections per hour of day and day of incubation was almost identical for the two samples, and weather at time of inspection was the same between samples. Females were sitting on first nests on 22 of 190 occasions (12%) and on second nests on 10 of 85 occasions (12%). This suggests that internal state during laying in first and second nests did not differ in ways relevant here. Support comes from Table 68, where data are segregated by date as well as nest number; 882 inspections are grouped into 5 samples: (1) first nests, 1 May-15 May; (2) first nests, 16 May-31 May; (3) second nests, 16 May-31 May; (4) second nests, 1 June-15 June; and (5) all other nests. Data in the three May samples appear homogeneous, with about half

TABLE 68
ATTENTIVENESS PRIOR TO LAYING OF FINAL EGG, ACCORDING TO NEST
NUMBER AND DATE OF LAYING

Nest number, ¹ date ²	Attentiveness ³	
	N	%
First nests, 1-15 May	36/247	14.6
First nests, 16-31 May	22/190	11.6
Second nests, May ⁴	10/85	11.8
Second nests, June ⁴	18/72	25.0
All other nests ⁴	75/288	26.0

¹ In numbering the individual's nests only those in which at least 1 egg was laid were counted.

² The date is that on which egg 1 was laid.

³ Attentiveness is measured by the nest inspection method described on page 197. The denominator is the number of nest inspections, and the numerator is the number of times the female was found on the nest.

⁴ Second nests in May all fell after 15 May, and few second nests in June fell after 15 June. Nests tabulated as "all other" received eggs in June and July.

as much attentiveness as in data from the two June subsamples, which appear homogeneous. Therefore again the difference seems related to date, not female state associated with nest number. Especially striking is the difference suggested between second nests in May and those in June.

If it is assumed on the basis of the foregoing that the environment in May was less conducive to attentiveness than in June, two related reasons may be proposed. (1) The difference may have been directly associated with cooler air temperatures in May; increased food requirements and/or greater difficulties in finding invertebrates (because less active) may have reduced female time on the nest. (2) Insects appeared to me to be more abundant in June than in May; if so, even on days of equal temperature females presumably could obtain energy more easily in June than in May and could allocate less time to foraging and more to incubating.

To test these points I (1) obtained for each nest inspection the mean air temperature on that day; (2) grouped inspections into May and June samples; (3) within each sample assigned each inspection to the mean temperature the day it was made, classifying temperatures among four equal intervals beginning at 16.1°C and proceeding to 26.7°C; and (4) separated inspections according to whether they were before or after 1230. Table 69 presents selected results; the breakdown according to temperature intervals is omitted because differences were nonsignificant. Percentages of attentiveness during both halves of the day were higher in June than in May; and within each temperature unit interval (June)

TABLE 69
PERCENTAGE OF ATTENTIVENESS¹ PRIOR TO LAYING OF FINAL EGG² IN MAY
AND JUNE ON DAYS WITH MEAN TEMPERATURES OF 16.1°-26.7°C³

	May		June	
	Inspections (N)	Attentiveness (%)	Inspections (N)	Attentiveness (%)
0600-1230	246	17.9	209	23.9
1230-1930	158	13.9	65	21.5

¹ Attentiveness is measured by the nest inspection method described on page 197.

² Data for all days of laying excluding the final day are pooled.

³ Within each month, attentiveness did not differ in the range of mean temperatures 16.1°-26.7°C.

TABLE 70
ATTENTIVENESS OF INDIVIDUAL FEMALES DURING DAY-LONG OBSERVATIONS
PRIOR TO LAYING OF FINAL EGG

Facts about attentive periods	Female A first nest 4 eggs, day 3, 17 May	Female B late nest 4 eggs, day 1, 2 July	Female B late nest 4 eggs, day 3, 4 July	Female C late nest 3 eggs, day 2, 6 July
Time first period began	0825	0630	0932	0549
Time last period ended	1906	1137	1728	1936
Before 0830				
N	1	3	0	4
Mean length, min	—	11	—	24
Extreme lengths	12	4-25	—	11-38
% time ¹ attentive	8	28	0	59
0830-1230				
N	5 ²	1	2	7
Mean length, min	11	—	53	20
Extreme lengths	6-16	9	46-60	2-35
% time ¹ attentive	22	4	44	59
1230-1630				
N	2	0	1	5
Mean length, min	12	—	—	21
Extreme lengths	9-15	—	35	1-42
% time ¹ attentive	10	0	15	42
1630-1930				
N	5	0	1	3
Mean length, min	8	—	—	10
Extreme lengths	1-17	—	35	7-13
% time ¹ attentive	23	0	19	17
Totals				
N	13 ²	4	4	19
Mean length, min	10	11	44	19
% time ¹ attentive	16.0	5.4	21.7	43.7

¹ Except as to female C, the day is regarded as beginning at 0600 and ending at 1930; see page 199. Female C's percentage is based on the interval between the beginning of her first and the end of her last attentive periods.

² Not included are two instances when this female went to the nest and looked into it for several seconds from the rim.

attentiveness was higher, even though not significantly. Thus in every comparison females were found on the nest slightly more often in June; therefore I do not reject the hypothesis that even at identical air temperatures laying birds were somewhat more attentive in June than in May. If they were, a seasonal difference in food abundance may be one reason. (There was significant variation in attentiveness according to date during the incubation period; see p. 211.) In addition to this possibility, differences in temperature, whatever the date, probably directly affected attentiveness on days of laying. Of 131 May inspections when daily mean temperatures were below 16.1°C, females were on the nest 12 times (9%); of 404 May inspections with daily means at and above 16.1°C, females were on the nest 66 times (16%); adj. Chi-square = 3.5; df = 1; 0.10 > P > 0.05. Although again the result is not significant, the corresponding data from the incubation period (p. 209) do show a significant difference and a similar relationship probably prevailed during laying and incubation.

Results, according to age: During laying there was no difference in attentiveness of yearlings and older females, either toward the first clutch or later clutches.

Data from nest watches.—Table 70 presents attentive data from 4 day-long watches, 1 on day 1 and 3 on the next-to-last day of laying. One nest was observed during 2 days. Percentages of attentiveness were calculated for the interval 0600–1930 for the reasons given on page 199, except for female C which went to the nest first at 0549 and left it last at 1936 to roost off the nest; attentiveness was therefore calculated for 0549–1936. Only on one day (17 May, female A) was weather a possible factor in attentiveness, and then for less than the full day; early in the morning rain fell for 2 hours, when the temperature dropped to 9.4°C.

The following points are noteworthy: (1) Female B's attentive time increased from 5% to 22% between day 1 and the next-to-last day of laying. (2) Female B (22% on 4 July) and female C (44% on 6 July) differed greatly in attentiveness on the next-to-last day, despite close similarity in all their known circumstances. Until 1230 on the day she laid her next-to-last egg, female C spent more time on the nest than off it. (3) The lowest percentage on the next-to-last day was 16%, on the day (in May) when the weather was unfavorable. (4) Most attentive periods during these four watches were much shorter than those recorded during the incubation period (compare Table 70 and Table 66), except for the intervals of female B on the day she laid egg 3. Between days 1 and 3 of laying, female B approximately quadrupled the percentage of time spent on the nest without increasing the number of attentive periods.

BEGINNING OF NIGHT ATTENTIVENESS

Females were never found on the nest at dusk except on the night before laying the final egg. On that evening I watched 29 nests from shortly before dusk until darkness. Four females did not go to the nest; 25 did so and were still present at nightfall. I returned to five of the latter nests next morning before daylight; the females were there, and I assume that they and other females that went to the nest at dusk spent the night there. I passed numerous other nests at dark on the day before laying of the final egg, and females were probably always present. I therefore estimate that the night before laying the final egg was spent on the nest in 90–95% of all cases.

Hour of arrival at nest.—I saw females arrive at the nest on 15 evenings. The earliest time was 1920 and the latest 2013; all but four fell between 1930 and 1949, and the mean was 1938.1 (SD 12.5 min). Comparison of the times with those at which females returned to the nest for the night during the incubation period (see the following section) reveals that they were about the same. Data were too few to show a correlation, if any, between times of roosting and civil twilight.

Once a male accompanied a female almost to the nest when she retired (see also pp. 228–229).

ATTENTIVENESS DURING INCUBATION PERIOD

Time of first inattentive period.—Of 30 observations of the first departure from the nest in the morning, the earliest was at 0453 and the latest 0734; the mean

was 0546.9 (SD 32.8 min). In this small sample no correlation of departure time with hour of sunrise appears, nor any suggestion of a relationship between departure time and advance of incubation, air temperature, precipitation, or cloud cover. Individuals probably differed in time of first departure. The range of all 30 times is 161 min; five birds observed more than once had the following ranges, with number of observations per individual in parentheses: 7 min (2), 21 min (5), 33 min (4), 46 min (5), 52 min (7, in 2 years). Another female left the nest at 0626, 0603, 0721 on three mornings; although the range is 78 min, all times are unusual in falling after 0600.

Walkinshaw (1959) saw a female leave a Michigan nest at 0549 EST, 43 min after sunrise.

End of last inattentive period.—I watched incubating females return to the nest for the last time of the day on 23 occasions; the earliest time was 1841, the latest 2021, and the mean 1943.2 (SD 24.7 min). The return at 1841 was unusual; the next earliest time was 1917. A correlation may exist between times of retirement and of civil twilight. In May no bird returned later than 1949 (compare the mean time for the full sample, 1943); and the latest return, 2021, was on 29 June. I detected no sign of correlation with other environmental factors.

The range of times covered only 64 min if the one exceptionally early case is omitted, and evidence of individuality is limited. However, the following seems suggestive: On 2 June and 9 June, a female retired at 1947 and 1948; on about the same dates, 3 June and 9 June, but in different years, another female retired at 2005 and 2011. The weather on all the days was about the same. But other individuals showed no consistency; for example, on four nights a female retired to the same nest at 1954, 2007, 1937, and 1917.

Walkinshaw (1959), in Michigan, saw a female retire at 1949 and 1915 EST on successive nights; on the latter night sunset was at 2029.

Length of active day.—The shortest of 20 active days (Table 66) was 715 min, the longest 903 min; the mean was 832.8 or 13 hours 53 min (SD 49.9 min). If for each of the 8 females watched on more than 1 day a mean active-day length is obtained and an overall mean then calculated from these 8 cases, that figure is 829 min. A mean day length per female is desirable because of indications (Table 66) that individuals differed: (1) Female 1's active days were 844, 847, 849, and 843 min long; the data were obtained at two nests in different years. Her earliest departure time was 0517, her latest 0545; her greatest daily attentiveness was 82.3%, her least 64.0%; her largest number of periods on and off per day 49, her smallest 31. Yet despite these considerable differences in other aspects of attentiveness on four days, length of active day differed by only 6 min. Approximately the same was true of female 4; and 2 each among the 3 active days of female 5 and female 6 were about the same length.

The active day of a female observed by Walkinshaw (1959) in Michigan lasted 806 min.

Length of interval of night rest.—In these calculations I assume females did not leave the nest at night, because on 20 of 22 all-day watches during the incubation period females were on nests as it grew light in the morning and were also there at dark. Many times I shone flashlights on nests at night, always finding the female incubating (compare Weeden 1966).

In six instances I saw a female's retirement and her first departure the next morning. Intervening intervals of night rest were 566, 567, 568, 568, 598, and 629 min long; the mean is 583 min (9 hr 43 min). Only three individuals were involved, which might account for some of the similarity among these times. A more representative figure may be one obtained by subtracting the overall mean active day length (829 min) from 24 hours: the difference is 611 min (10 hours 11 min). Based also on subtraction, the mean interval of night rest of female 6 (Table 66) was 673 min, longer than any interval directly observed; and female 7 may have spent only 537 min on the nest at night.

Walkinshaw (1959), in Michigan, saw a female go to the nest at night and leave it 629 min later.

Attentiveness during 24-hour day.—When assumed attentiveness during darkness is added to observed time on the nest during day-long watches, the greatest time a female was attentive was 1302 min (90%) of a calendar day; on the day of least attentiveness a female incubated 1136 min (79% of 24 hours). The mean for the 20 watches that can be used for this calculation was 1248.0, or 20 hours 48 min (SD 46.8 min), or 86.7%. Times reported by Walkinshaw (1959) for a female he watched in Michigan during daylight indicate she was attentive for 89.3% of 24 hours.

Most investigators report attentiveness only for the daylight interval or part of it. Hereafter, unless the contrary is noted statements about attentiveness of Prairie Warblers will refer only to the daylight period, as defined in the next subsection.

Attentiveness during daylight.—Since data are not numerous enough to show a relationship between length of active day and time of civil twilight, I have disregarded changing photoperiod in calculating percentage of daylight attentiveness. This greatly simplifies analyses and comparisons. The day is treated as beginning at 0430 and ending at 2030 (960 min). To justify these times: a Prairie Warbler sang as early as 0435, and other passerines often sang considerably earlier; 2030 is about the time of the latest Prairie Warbler song (see Fig. 9) and is 9 min later than the latest time a female ended her active day.

Based on the nest-watch method (p. 197), among 20 cases the most attentive and the least attentive birds incubated 822 min (86%) and 656 min (68%) of the daylight period. The mean was 768.0 or 12 hours 48 min (SD 46.9 min), or 80%. The nest-inspection method yields a very similar mean: On 2040 inspections, I found females on the nest 1601 times (78.5%). Both estimates of attentiveness are probably slightly low, because the early days of the incubation period contributed a disproportionate share of the data. Seven nest watches fell on day 1, when attentiveness was lowest (see below); and since many nests failed early in incubation (Chapter 33), more inspection data were collected from the beginning of the period than later.

A female observed by Walkinshaw (1959), in Michigan, was attentive 84% of the period 0430–2030.

Variation according to advance of incubation.—The most useful information on this variation is provided by nest inspections, which indicate that attentiveness reached full development on day 3 of the period (compare Kendeigh 1952: 27, Weeden 1966: 374). I divided the incubation period into four segments each 3 days long, except that variation in hatching time made the final segment, which

TABLE 71
ATTENTIVENESS¹ ACCORDING TO DAY OF INCUBATION PERIOD AND NEST NUMBER

Day of incubation period	Nest number ²			Totals
	1	2	3 and later	
1				
N	76/115	51/66	75/109	202/290
%	66	77	69	69.7
2				
N	62/85	37/49	74/97	173/231
%	73	76	76	74.9
3				
N	62/82	37/43	71/82	170/207
%	76	86	87	82.1
4-6				
N	174/227	78/92	187/226	439/545
%	77	85	83	80.6
7-9				
N	133/164	69/85	174/207	376/456
%	81	81	84	82.5
10-12 ³				
N	96/126	33/47	112/138	241/311
%	76	70	81	77.5

¹ Attentiveness is measured by the nest inspection method described on page 197. The denominator is the number of nest inspections and the numerator the number of times the female was found on the nest.

² In numbering the individual's nests, only those nests in which at least 1 egg was laid were counted. Nests whose number was unknown and second-brood nests are treated as 3 and later.

³ Data from females that incubated more than 12 days are included.

for present purposes ended with the day before hatching began, somewhat variable in length. When data (from Table 71) for the four segments are tested for independence, Chi-square = 11.3; df = 3; $P < 0.01$. The principal source of this variation fell at the very beginning of the period. To show this, Table 71 reports results for 1-day units of the first segment. Females were present on 69.7% of inspections on day 1, 74.9% on day 2, and 82.1% on day 3. Attentiveness increased between days 1 and 3 at all nests, regardless of the number previously built that season; the increase varied between 9% and 18%.

Day-long nest watches also reveal attentiveness as lowest on day 1 (mean percentage for 7 watches, 70.5%; mean for 15 later day-long watches, 78.6%). Added corroboration comes from 4- and 5-hour watches on the morning of day 3 at all 4 nests whose attentiveness on day 1 was below 70% (Table 66): These shorter watches show a 7-12% increase on day 3, with no environmental reasons apparent.

Day 1 and later days differed most greatly in amount of time spent on the nest before 0830, as Figure 17 (based on results of all 22 day-long watches) illustrates. For each quarter of day 1, attentiveness was lower than during the corresponding quarter of subsequent days, but the difference became steadily smaller as day 1 progressed (percentages are calculated to eliminate effect of the fact that two females roosted off the nest before laying the final egg). In short, attentive behavior reached full development gradually, not only in terms of 1-day units of time but also within day 1 of the incubation period (compare Hinde 1952: Table 21).

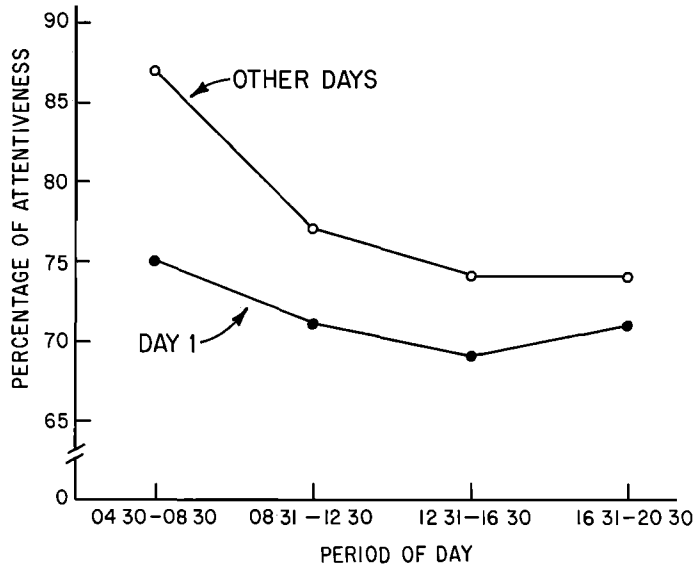


FIGURE 17. Percentage of attentiveness of incubating females per 4-hour segments of the day; day 1 of incubation compared to all other days. Data for day 1 are based on seven day-long nest watches; see text. Data for other days are based on 15 day-long nest watches.

Table 71 suggests that attentiveness, as determined by inspections, was somewhat lower during the last 3 days of the incubation period than between days 4 and 9 (inclusive), but the difference was not significant. Day-long watches of females 1, 4, 5, and 6 (Table 66) on the day before eggs hatched reveal no greater inattentiveness that day; e.g. females 5 and 6 spent more time on the nest just before hatching.

The mean of 15 all-day watches probably is a more reliable estimate of female attentiveness from day 4 onward (76.6%) than the data from inspections (on most days above 80%), because inspections were slightly more frequent at hours when attentiveness was greatest. During only five all-day watches was the female on the nest as much as 80% of the time.

Variation according to hour of day.—Figure 17 reveals, for the approximately 4-hour-long intervals of daylight, that females incubated most during interval 1, became steadily less attentive in the next two intervals, and in interval 4 spent as much or a little more time on the nest than during the preceding interval. When the same data are plotted according to 1-hour intervals this picture changes considerably. Figure 18 presents separate curves obtained from nest watches and nest inspections. Each 60-min period begins 30 min before the clock hour (0700 begins at 0630, etc.). In the curve for nest watches the two females that did not spend the night on the nest before laying egg 1 were ignored in calculating the percentage for 0500.

Disregarding for the moment percentage differences in the two curves, their shapes are similar, showing a decline in attentiveness between dawn and mid-morning, then an increase that continued for 2 hours, a long and nearly steady decline between midday and 1700, and a steep rise prior to nightfall. The only

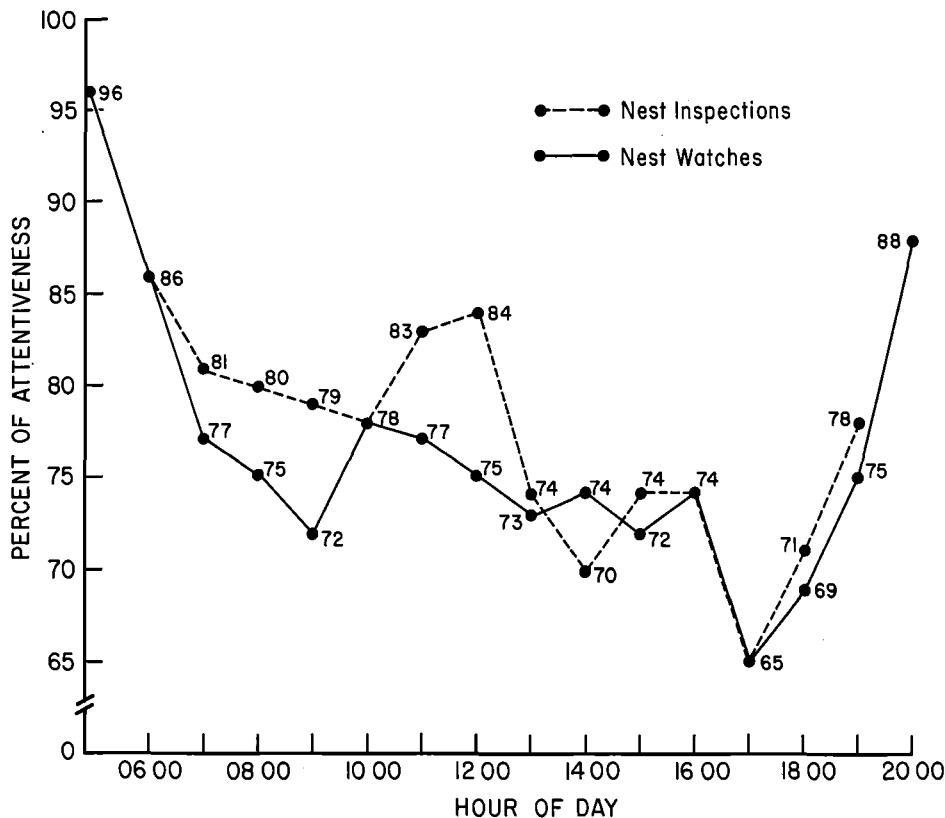


FIGURE 18. Percentage of attentiveness of incubating females according to hour of day, as determined by nest-watch and nest-inspection methods (see text). Time is eastern standard. Hours run from 30 min before to 30 min after the times designated, e.g. 0630-0730.

inconsistencies are the slightly different times at which some of these changes began. The generally lower percentages of attendance as determined by nest watches are attributable to the large number (7 of 22) on day 1 of the incubation period; in comparison, 296 of 2040 inspections were on day 1. Thus the higher hourly percentages shown by the nest-inspection method are probably more accurate estimates of attentiveness over the full incubation period.

Greater attentiveness just after dawn and again preceding nightfall describes the behavior of many female passerines (see Weeden 1966: 382). The late-morning rise in my data may have resulted in part from gradual satiation of hunger after the night's fasting. At some nests it was also in part observably attributable to increased heat and exposure to sun, which caused females to shade nests in late morning (see pp. 209-210). However, these suggestions leave unexplained the decline in attentiveness during the afternoon; nests were as exposed at 1400 as at 1100, and air temperatures were almost always higher (see Visser 1944: 81). Kendeigh (1952: 73-75), Hinde (1952: 120), Armstrong (1955: 175-183), and others have accounted for greater afternoon inattentiveness in some passerines by pointing to higher air temperatures. Kendeigh (1952: 73-75) found that attentive-

ness of House Wrens decreased hardly at all during afternoons of cool days but did so markedly on warm afternoons. My watches reveal no such relationship; on two rather cool days (mean temperatures 12.2°C and 13.3°C) females exhibited the usual reduced afternoon attentiveness. Indeed, the most pronounced hourly decline in attentiveness (from 77% during 0800–1200 to 67% during 1200–1600) was in May, the coolest month of the breeding season; in June and July (pooled) for the same two quarters of the day the corresponding percentages were 82% and 79%. In the Prairie Warbler, attentiveness declined in the afternoon probably because normally food needs can be satisfied most readily then and with least loss of heat by eggs (see Verner 1965). This may also explain the larger difference between morning and afternoon attentiveness in May; if, as suggested (p. 201), food was more difficult to obtain in May, this could have considerably increased time spent off nest in the afternoon. In addition, on unusually hot days, which were commoner in June and July, heat may have minimized the difference between morning and afternoon attentiveness because of the need to shade eggs during the hottest (afternoon) hours.

Variation according to air temperature.—To pursue the relationship between attentiveness and air temperature just suggested, I distributed nest inspections according to mean temperature on day of inspection (hourly temperatures were not available), dividing temperatures into unit intervals of about 5.5°C. Table 72 shows that females spent less time on the nest at low than at moderate temperatures (Chi-square = 40.6; df = 4; $P < 0.001$). On the very hottest days attentiveness apparently declined, a fact perhaps related to the lesser dependence of eggs on application of heat by the female (see Kendeigh 1952: 42–43, 74). Kendeigh (*loc. cit.*) suggests that House Wrens may have been less attentive on very hot days because of discomfort of incubating, but the evidence is to the contrary in the Prairie Warbler. The most sustained attentiveness was by birds obviously suffering because of the heat (compare Mayfield 1960: 94, Franks 1967; see the next subsection).

The daily mean temperature interval at which attentiveness was greatest (15.9°–27.0°C) prevailed on most days of the months during which Prairie Warbler nests contained eggs: 84% of all inspections were made on such days, and I inspected nests virtually every day.

Much variation in attentiveness with changing temperature was independent of date. Data from May, when range of temperatures was greatest, illustrate this best. On May days with means below 15.8°C, females were on nests on 114 of 185 inspections (62%); at temperatures over 15.9°C, they were present on 466 of 596 inspections (78%). Compare these percentages with those for the full season in Table 72.

In unusually cool weather attentiveness may have dropped below 50%. On 15 midmorning inspections on 26 and 27 May 1961, when the temperature was 4.4°C, I found females on 5 nests. Assuming these data are representative, the lower rate may have retarded development (see p. 236) and was probably a response to difficulty in meeting the female's food requirements.

Variation according to exposure to sun.—If observation intervals no longer than 3–4 hours are considered, exposure of the nest to the sun on hot days caused females to become much more attentive. To take a representative case, female 4

TABLE 72
PERCENTAGE OF DAILY ATTENTIVENESS¹ DURING INCUBATION PERIOD,
ACCORDING TO DAILY MEAN TEMPERATURE

Daily mean temperature	Inspections N	Attentiveness %
10.2°C	37	59.5
10.3–15.8°C	154	59.1
15.9–21.4°C	685	79.9
21.5–27.0°C	1018	78.9
27.1–32.5°C	146	73.3

¹ Attentiveness is determined by the nest inspection method described on page 197.

(Table 66), whose nest was very exposed in late morning, on 5 days in the period 3 June–13 June spent the following percentages of the interval 1000–1230 on the nest (in chronological order with noon temperature at my observation post in parentheses): 71% (21.1°C), 81% (23.3°C), 85% (25.6°C), 91% (32.2°C), 90% (27.8°C). The first, rather low, percentage was probably affected by the fact that the day was day 1 of the incubation period (see pp. 213 and 219 for additional data from these same 5 days).

Despite the short-term effect of exposure and heat, just shown, the proportion of the full day spent on the nest apparently was little affected. Thus female 4's full-day attentiveness on the same 5 days never exceeded 80% (compare with Tables 66 and 71). Evidently she compensated for sustained shading at midday by modifying her regimen thereafter (see also the next paragraph and p. 213).

Variation according to rainfall.—A few times females returned to the nest when heavy rain began and left when it stopped, but even such short-term effects were rare and probably were compensated for by reduced attentiveness later in the day. The slight importance of falling rain is indicated by a watch (female 2, Table 66) during which it rained constantly, often hard, from 0445 through 1445. The female incubated 84%, not a high figure for that segment of day 9. Six days earlier, between 0750 and 1200 in fair weather, she had been attentive 79% of the time; during those hours on the rainy day she was attentive 80%. Nest-inspection data tend to confirm this result but are more applicable to a wet environment than to falling rain. Inspections on dry days and days when at least 5 mm of rainfall were recorded show no significant differences, as is also true when rainy days and dry days are broken down according to temperature intervals.

TABLE 73
ATTENTIVENESS¹ DURING THE INCUBATION PERIOD, ACCORDING TO MONTH
AND NEST NUMBER²

Attentiveness	Month			Nest number		
	May	June	July	1	2	Other ³
N	580/781	617/807	370/452	603/799	305/382	693/859
%	74.3	76.5	81.9	75.5	79.8	80.7

¹ Attentiveness is measured by the nest inspection method described on page 197. The denominator is the number of nest inspections, and the numerator is the number of times the female was found on the nest.

² In numbering the individual's nests only those in which at least one egg was laid were counted.

³ This category includes nests subsequent to second nests, nests subsequent to first nests whose number is unknown, and second-brood nests.

TABLE 74
ATTENTIVENESS¹ DURING THE INCUBATION PERIOD ON DAYS WITH DAILY
MEAN TEMPERATURES OF 18.9°–23.9°C, ACCORDING TO MONTH

Month	Attentiveness	
	N	%
May	292/371	78.7
June	327/410	79.8
July	167/200	83.5

¹ Attentiveness is measured by the nest inspection method described on page 197. The denominator is the number of nest inspections, and the numerator is the number of times the female was found on the nest. See text, this page.

Variation according to date and nest number.—Attentiveness per month increased steadily from 74% in May to 82% in July ($P \approx 0.01$), as shown by nest inspections (Table 73). The table also reveals an increase, though smaller and less steady, between attentiveness at first, second, and later nests ($P < 0.025$). Ascending nest number inevitably also involves advancing date, and Table 73 therefore raises the question whether date and nest number were independently important. It was proposed above (p. 202) that variation in attentiveness during laying was a function only of advancing date, and the same appears clearly to be true of the increasing attentiveness during the incubation period: Inspection results from only those days on which I examined at least one first and one second nest yield samples approximately alike as to date, time of day of inspection, and weather, although for any date and hour of day numbers of inspections of first nests (166) and second nests (119) differed somewhat. For both samples attentiveness was 77%; nest number therefore appears irrelevant.

Turning to date as a predictor, the seasonal increase of time spent incubating probably cannot be fully explained by the rise in temperature. Although temperature may have been the principal proximate factor, even when comparison is restricted to days with about the same mean temperature, attentiveness may have risen as months passed. Inspections on days with mean temperatures between 18.9°C and 23.9°C show 79% attentiveness in May, 80% in June, and 84% in July (Table 74). Though not significant, the rising trend, in conjunction with this same trend during laying, suggests an effect independent of mean temperature. Reasons for this have been proposed on pages 201–202.

Variation according to other factors.—Attentiveness of yearling and older females did not differ significantly, although in both analyses that were made yearlings were on the nest a slightly higher proportion of times (on first nests 75% as compared to 71% for older females, on all later nests 83% as compared to 79% for older females).

Behavior or presence of the male seemed to have little or no effect on daily percentage of attentiveness, as indicated by day-long observations at nests of three females that had no mate during at least 1 day of observation. Female 6 (Table 66) was attentive 77% of day 3, when her mate was present, and 78% of day 7, by which time he had disappeared. Female 3 (Table 66) lost her mate between a day when she was attentive 82% and a later day when the figure was

also 82%. Female 8 (Table 66), which had no mate, incubated 77% of day 10; this percentage is near the overall average. However, Table 66 does suggest that females without mates tended to have fewer attentive and inattentive periods per day than did birds with mates; compare Kendeigh 1952: 40, 44–46.

It was proposed above (p. 204) that length of active day varied individually, and the same may have been true of number and duration of attentive and inattentive periods (see following section). Individuality in daily percentage of attentiveness is suggested by the consistently high attentiveness of female 3 (Table 66).

NUMBER OF ATTENTIVE AND INATTENTIVE PERIODS PER DAY

This section is based primarily on the long nest watches. In analyzing periods at and away from the nest I ignored a few of less than 1 min when females left the nest to repel an intruder, remove an approaching cicada, etc. Sometimes when nests were exposed to the sun, females left only briefly and foraged nearby for as little as 1 min. I counted these as inattentive periods.

The greatest number of attentive periods during a day (Table 66) was 24, the smallest 9. The mean for 22 days was 17.0 (SD 4.1); the mode (3 cases) was 19. When the female spent the night on the nest, inattentive periods numbered 1 more than attentive periods. Extreme numbers of inattentive periods were 25 and 10, the mean (20 days) 18.0 (SD 4.2), and the mode 20. (The extremes were unaffected by the fact that two females did not remain on the nest the night before nest watches.) A female watched all day by Walkinshaw (1959) in Michigan had 9 attentive and 10 inattentive periods.

Of special interest is a long watch (not shown in Table 66) on day 1 on the incubation period of a female that abandoned her nest at 1743. Attentive behavior early in the day may have been unaffected by whatever factors (see below) led her to desert; if that is true and if her periods were normal during a substantial part of the day (i.e. typical for her), they differed greatly from any other observed regimen. By 1230, this bird had combined 42 attentive and inattentive periods while incubating a normal amount of time since 0430, viz. 78%, a percentage suggesting that the rhythm of periods may have been typical for her. The longest attentive period was 30 min, the shortest 6 min, and the mean 15 min. Inattentive periods were unusually consistent, with extremes of 3 and 8 min (compare Table 66) and a mean of 5 min. From 1230 to 1630 the female incubated only 50% of the time with a combined total of 20 attentive and inattentive periods. At 1638 she suddenly began to reduce the length of attentive periods (to 2, 4, 4, 3 min) but not of inattentive periods, and at 1743 she deserted. The only apparent reason was that the nest held just one egg; I climbed to it at 1830 and found that the other three had disappeared sometime before dawn. I had watched from a spot far from the nest and probably had not affected the female's behavior.

Variation according to individual differences.—Against the background of great variation in numbers of attentive periods per day, just shown (see also discussion of lengths of periods, below; compare Weeden 1966: 372–374), the day-to-day consistency of certain females suggests individuality. Thus, female 5's daily at-

tentive periods on 4 days numbered between 11 and 14; female 4 had 17 to 22 periods on 3 days. Female 6 was less consistent, with 14, 18, and 21 attentive periods on days in the middle of the incubation period.

Variation according to advance of incubation.—Three among the four females (Table 66), each watched at least 3 days at a single nest, made consistent (i.e. one-directional) changes in number of attentive periods as incubation advanced. Female 1 and female 5 increased the number of periods, while female 6 steadily decreased the number. Another bird, female 3, watched on days 1 and 8 at each of two nests, reduced the periods on day 8 in each case. Female 4 showed no one-directional tendency, changing from 22 (day 1) to 17 (day 7) and back to 22 (day 11).

Kendeigh (1952: 27) found that female House Wrens tend to increase periods per day for at least the first 8 or 9 days of incubation.

Variation according to weather.—With only 22 all-day nest watches, most of them when daily mean temperatures were moderate, I detected no correlation between number of periods and air temperature (compare Kendeigh 1952: 41, Weeden 1966: 374, 376–377).

Females prolonged attentive periods and abbreviated inattentive periods when nests were directly exposed to sun but seemed to compensate by modifying lengths and therefore numbers of subsequent periods. For example, female 4 (Table 66) at 1013 began a very long attentive period of 102 min; but her next three were 6, 9, 10 min, and the total number for the part of the day involved was about average. She also appeared to make up later for the brevity of her off-the-nest periods when the nest had been in the sun: Her inattentive periods during the middle of the day (beginning at 1155) lasted 1, 1, 3, 1, 1, 3 min, respectively. At 1738, when many females began to abbreviate their inattentive periods, she took an inattentive period of 24 min and shortly thereafter another of 30 min. I detected no correlation between length of attentive period and immediately succeeding or preceding inattentive periods (compare Cox 1960: 19).

Sudden very heavy rains probably sometimes caused attentive females to stay on the nest longer than they otherwise might have and occasionally seemed to stimulate inattentive females to return; but most heavy rains were brief and are not likely to have had much effect on number of periods in the full day. Even during prolonged rain, rare during the breeding season, number of periods appeared unaffected. For example, on a clear day female 2 (Table 66) took an aggregate 22 attentive and inattentive periods by 1456; 8 days later in a steady rain she took 22 periods by 1445. During a 4-hour watch of her nest on a rainless morning on yet another day she had a total of 13 periods, on the rainy day during the same 4 hours, 11 periods.

Relationship between number of periods and other measures of attentiveness.—Since active-day length of the individual female varied little (p. 204) and no female had the same number of periods on all days she was observed, no close correlation is evident when periods per day are plotted against active-day length in the 19 cases (Table 66) for which the data are available. However, lack of correlation is probably attributable to the unequal numbers of day-long observations per female: When data from 1 day per female (Table 66, asterisks, 8 cases in

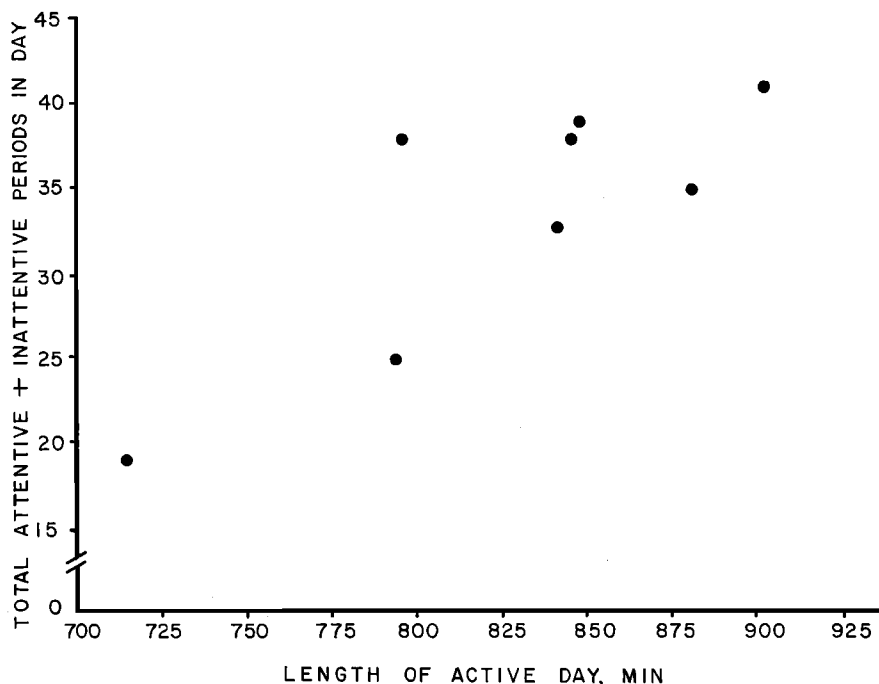


FIGURE 19. Total female attentive and inattentive periods per day during eight selected day-long nest watches in the incubation period, according to length of active day; see text.

which active-day length is known) are plotted, a positive correlation appears (Fig. 19) between day length and number of periods; $r_s = 0.81$; P (one-tailed) < 0.01 . Kendeigh (1952: 48) says that the more nervous the female House Wren or the higher her metabolic rate, the more numerous and short are her periods, the earlier she begins activity in the morning, and the later she ceases it in the evening. As will be seen (p. 219), female warblers that had many periods in a day also had shorter periods. Therefore three of the variables (I know nothing about nervousness and metabolic rate) that Kendeigh found associated in the wren were probably also associated in the warbler.

When the seven watches on day 1 of incubation are ignored (because attentive behavior had not reached full development) no correlation existed between daily percentage of attentiveness and total number of attentive and inattentive periods.

Relationship between number and length of periods is discussed in the following section.

LENGTH OF PERIODS

Table 75 distributes 400 attentive periods from the 24 long nest watches (Table 66) among 5-min unit intervals of length; 422 inattentive periods are assigned to 3-min unit intervals. (Final intervals are larger than 5 and 3 min in order to include a few unusually long periods while avoiding extending the table.) Table 75 also presents lengths of periods on the 10 days selected to provide one watch per female. Regardless of whether unequal representation of individuals biases the larger

TABLE 75
DURATION OF ATTENTIVE PERIODS AND INATTENTIVE PERIODS DURING
DAY-LONG¹ NEST WATCHES IN THE INCUBATION PERIOD

Attentive periods			Inattentive periods		
Interval length, min ²	Number of cases		Interval length, min ²	Number of cases	
	All watches ³	10 selected watches ³		All watches ³	10 selected watches ³
2-5	3	0	1-3	12	2
6-10	8	2	4-6	67	32
11-15	14	6	7-9	91	27
16-20	25	6	10-12	84	43
21-25	51	21	13-15	55	18
26-30	71	20	16-18	38	16
31-35	61	26	19-21	28	11
36-40	45	23	22-24	24	9
41-45	40	20	25-27	6	3
46-50	23	9	28-30	7	3
51-55	12	4	31-61	10	4
56-60	14	8			
61-65	12	7			
66-70	7	3			
71-75	5	1			
76-123	9	4			
Total	400	160	Total	422	168
Mean	35.8	37.9	Mean	12.5	12.7
SD	16.7	16.6	SD	7.2	6.6
C ⁴	0.47	0.44	C ⁴	0.57	0.52

¹ Two watches lasted less than the full day; see page 197.

² Fractions of a minute were rounded to the nearest whole.

³ The total number of watches, 24, includes several cases of females and nests observed on more than 1 day; 7 watches were on day 1 of the incubation period. Ten watches were selected to include only 1 per female and, except for 2 of them, to exclude day 1 of the incubation period.

⁴ C is the coefficient of variation.

sample, the sample of 10 is probably more representative of the whole incubation period, because only two of the watches took place on day 1.

For the large sample, extreme lengths of the attentive periods were 123 and 2 min; the mean is 35.8 min (SD 16.7 min), the median 32 min. The modal interval, 26-31 min, includes 18% of the periods and the interval 31-35 min includes an additional 15%. Extreme inattentive periods were 61 and 1 min; the mean is 12.5 min (SD 7.2 min), the median 11 min. The modal interval, 7-9 min, includes 22% of the periods; the interval 10-12 min, with 20%, approaches the mode.

For the smaller sample the mean of 160 attentive periods is 37.9 min (SD 16.6 min); the median is 33 min; the mode is 31-35 min. The 168 inattentive periods lasted a mean 12.7 min (SD 6.6 min); the median is 11 min. The mode is substantially different from that of the larger sample; 26% of the periods lasted 10-12 min.

Table 75 reveals important characteristics of the distributions: All are somewhat skewed, with means larger than medians and medians as large as or larger than modes. Toward the positive end of the curve are long tails, somewhat concealed in the table by the larger final unit intervals for both kinds of periods. Frequencies are heavily concentrated in a relatively short segment of the scale;

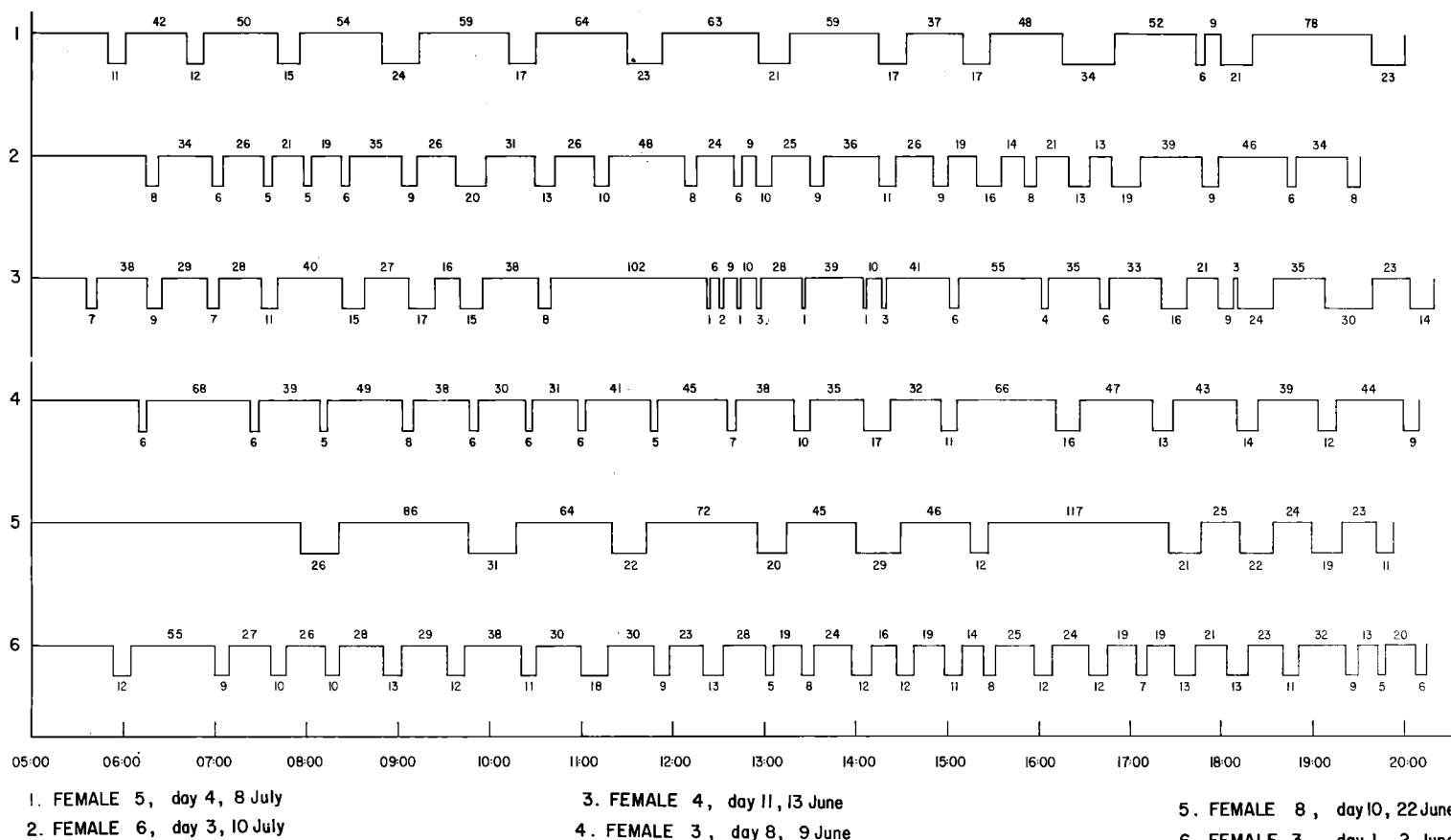


FIGURE 20. Attentive-inattentive rhythms of selected incubating females at nests watched throughout the day. Time (eastern standard) is shown at the bottom. Hours run from 30 min before to 30 min after times designated, e.g. from 0630-0730. Each jagged line represents 1 day; upper segments indicate attentive periods, lower segments inattentive periods; numbers show lengths of periods in minutes. Designations of females, day of incubation period, and date refer to Table 66.

see especially attentive periods for the 10 watches. Variation in attentive periods is less than in inattentive periods, as indicated by the coefficients of variation.

Variation according to individual differences.—Examples of rhythms of individual females on selected days (Fig. 20) may reflect individuality. The slow regular rhythm of female 5 (line 1) and the rapid regular rhythm of female 6 (line 2) suggest differences in temperament; these watches were only 2 days apart, in similar weather, on day 3 and day 4 of incubation of the respective females. Equally suggestive is similarity in behavior of the same individual on different days, e.g. in the rhythm of female 3 on day 8 at 2 different nests (not shown in Fig. 20; see Table 66). However, females sometimes behaved differently from one day to another at the same nest, even apart from differences associated with the beginning of the incubation period: The median attentive period of female 6 (Table 66) on day 3 of incubation was 26 min and on day 11 was 33 min.

Variation according to time advance of incubation.—Both a lengthening of attentive periods and an abbreviation of inattentive periods produced the increase in percentage of attentive time between day 1 and the middle of the incubation period. To investigate this point I selected two samples: (1) pooled data from day 1 of the incubation periods of female 1 (on 17 May; see Table 66), female 3 (on 2 June), female 4, and female 5; and (2) pooled data from the next day-long watch at the same nests of these females. The median attentive period on day 1 was 27.9 min long, on the later day 38.3 min long; in a median test, adj. Chi-square = 14.4; $df = 1$; $P < 0.001$. The median inattentive period decreased from 12.8 min on day 1 to 9.9 min on the later day; in a median test, adj. Chi-square = 6.2; $df = 1$; $P < 0.025$.

As expected (p. 207), a test of pooled numbers of attentive and inattentive periods from day 3 of female 6 and day 4 of female 5 (Table 66) against pooled numbers from day 11 of these females showed no change in length of periods.

Variation according to hour of day.—Table 76 analyzes pooled data from all 24 long watches; results from the 10-day sample did not differ appreciably and are not shown. Each attentive and inattentive period was assigned to the hour in which it began; hourly intervals are those described on page 207. Determination of modal period length per hour was as follows: For attentive periods, I selected the 10 min in which the greatest number of cases fell; but if this 10-min interval could be shortened without eliminating any case, I reduced it as much as possible. For example, if 12 periods lasted between 30 and 38 min and no periods were 29 or 39 min long, the mode is stated as 30–38 min. Inattentive data were similarly treated, except that the maximum interval length is 5 min.

Figure 21 graphs median period-lengths per hour and reveals marked variation, as expected from the variation in percentage of attentiveness during the day (Fig. 18). To summarize chronologically: (1) Attentive periods were longest and inattentive periods shortest between daylight and 0600 (note again that 0600 ended at 0630). (2) Attentive periods shortened considerably at 0700, then lengthened steadily to a second peak at 1000. Meanwhile inattentive periods grew progressively longer until 1000, both absolutely and relative to rate of increase in duration of attentive periods. (3) Attentive periods became steadily shorter from 1000 until 1300, then changed little during the rest of the day. Inattentive periods underwent similar abbreviation from 1000 to 1200, thereafter grew constantly

TABLE 76
ATTENTIVE AND INATTENTIVE PERIODS,¹ ACCORDING TO HOUR OF DAY
DURING THE INCUBATION PERIOD

Attentive periods ²								
Hour ^a	N	Mean	Extremes	SD	C ⁴	Median	Mode ⁵	
							Interval	Cases
Before 0630	29	42.7	19-68	13.8	0.33	41	28-36, 38-47	9
0700	25	35.9	12-81	13.2	0.37	34	26-35	12
0800	31	38.3	19-86	16.3	0.43	35	24-30	12
0900	29	36.1	13-65	12.1	0.34	36	31-39	14
1000	25	44.8	24-108	21.9	0.49	38	30-38	13
1100	27	40.5	15-72	15.2	0.38	35	26-34	11
1200	31	33.5	5-87	17.5	0.52	32	21-28	10
1300	30	32.6	2-59	12.9	0.40	30	21-30	12
1400	30	35.3	10-70	15.7	0.45	31	21-30	11
1500	29	36.6	11-123	28.2	0.77	27	18-27	9
1600	28	32.3	14-71	15.9	0.49	30	21-30	14
1700	27	30.2	13-63	12.7	0.42	28	19-28	11
1800	34	33.1	3-72	17.0	0.51	31	20-29	12
after 1830	24	28.5	9-44	9.4	0.33	28	23-34	12
Inattentive periods ²								
Before 0630	28	8.2	3-24	4.1	0.50	7	5-9	22
0700	30	13.0	2-61	11.0	0.84	10	6-10	16
0800	29	10.7	3-26	5.1	0.47	10	12-16	12
0900	31	13.3	4-32	6.2	0.47	12	6-9	14
1000	24	13.5	6-31	6.7	0.50	12	6-9, 11-14	8
1100	28	13.9	5-35	7.1	0.51	11	10-14	12
1200	30	10.9	1-23	6.4	0.58	10	6-10	10
1300	30	12.0	1-28	6.6	0.55	12	5-9, 8-12, 12-16	10
1400	33	12.2	1-29	6.6	0.54	11	9-12	14
1500	28	13.5	6-28	5.2	0.39	13	12-16	11
1600	31	15.9	4-34	9.3	0.58	14	6-10, 8-12, 12-16	9
1700	26	15.5	4-24	6.3	0.41	15	11-14	8
1800	30	15.1	6-48	8.6	0.57	13	7-11	10
After 1830	44	10.1	4-30	5.6	0.55	9	4-8	21

¹ Data were obtained during the 24 long nest watches summarized in Table 66.

² Measurements are in minutes, with fractions rounded to the nearest whole. Periods were assigned to the hour in which they began.

³ Hours began 30 min before the time shown; e.g. 0700 began at 0630 and ended at 0730.

⁴ C is the coefficient of variation.

⁵ Modal intervals were determined as described on page 217; lengths of intervals are inclusive.

longer to reach a maximum at 1700. Thus, declining afternoon attentiveness (p. 207) was produced by relatively short attentive periods of stable hourly median length, accompanied by increasingly long inattentive periods. (4) From 1700 until dark, inattentive periods became shorter, very much so in the final hour of the day. In contrast to this pattern, the Mourning Warbler's increased attentiveness late in the day is the result of both lengthened attentive periods and abbreviated inattentive periods (Cox 1960: 18). Weeden (1966: 374), studying the Tree Sparrow in Alaska, found that inattentive periods remained relatively constant and fluctuations in percentage of attentiveness during the day were produced by variation in attentive periods.

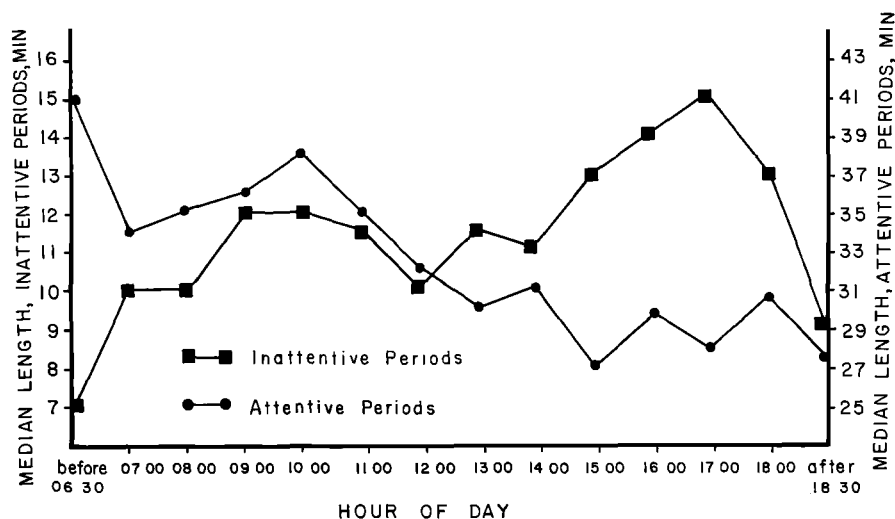


FIGURE 21. Median length of attentive and inattentive periods according to hour of day. Time is eastern standard. Hours run from 30 min before to 30 min after the times designated, e.g. from 0630–0730. Data are taken from 24 day-long nest watches described on page 197 and summarized in Table 66.

Table 76 may show a tendency for another kind of change. Hourly coefficients of variation for attentive periods reveal lowest relative variation prior to 0800. Thereafter, these coefficients alternately rise and fall, but rises grow steadily greater and declines smaller with the progress of the day. This trend is not reversed until 1600; data from 1900 until dark are about as consistent as those of early morning. Inattentive data exhibit no discernible pattern.

Variation according to weather.—No day-long statistical relationship between air temperature and length of periods is revealed by my few watches. But short-term effects of heat and exposure on periods are suggested by the following, which are lengths of female 4's first attentive and first inattentive periods after 1000 on each of the 5 days referred to on pages 209–210 (where the relevant weather information is presented): attentive 41 min and inattentive 10 min; attentive 79 min and inattentive 4 min; attentive 61 min and inattentive 8 min; attentive 83 min and inattentive 1 min; attentive 102 min and inattentive 1 min.

The possible temporary effect of rain is described on page 210.

Relationship of lengths of day's attentive periods to lengths of inattentive periods.—When median length of the day's attentive periods is tested for correlation with median length of its inattentive periods during each ($N = 17$) long nest watch carried out on or after day 3 of the incubation period, $r = 0.71$; $df = 15$; $P < 0.01$ (compare Cox 1960: 18). Although the absolute increase in median attentive period was greater than the associated increase in length of median inattentive period, daily percentage of attentiveness declined as the two medians increased; that is, the ratio of length of median attentive to median inattentive period shifted in favor of the latter.

Length of periods related to number of periods.—As expected, a negative relationship existed between aggregate number of periods per day and median lengths of at-

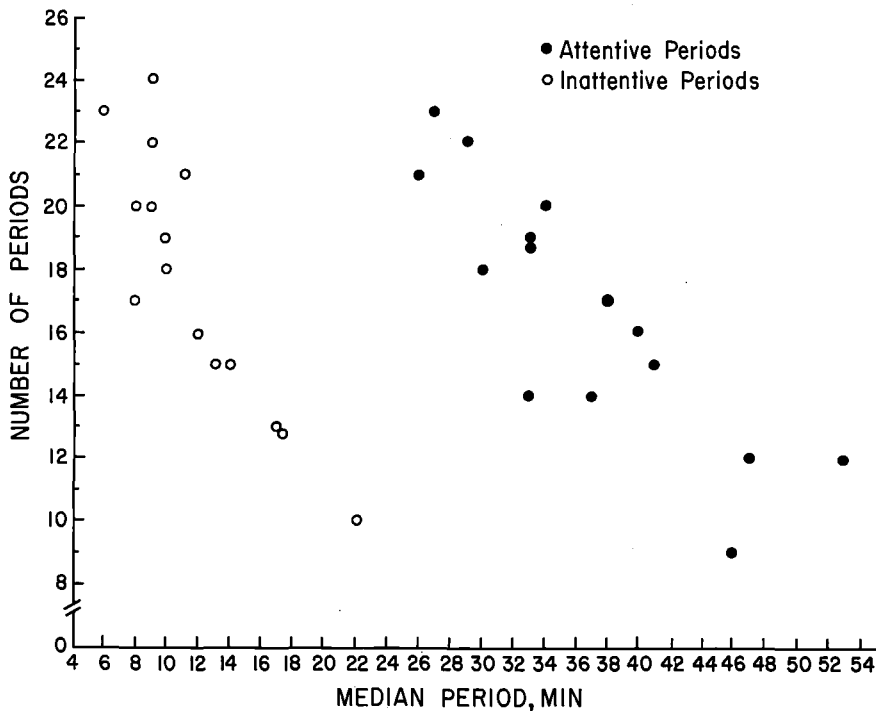


FIGURE 22. Median length of day's attentive and inattentive periods during incubation, plotted against numbers of periods per day. Data were obtained during 15 day-long watches from day 3 of the incubation period until the end of that period.

tentive and inattentive periods (despite the positive correlation between number of periods and length of active day; see p. 214). Figure 22 illustrates this by plotting median length of each day's attentive periods and inattentive periods against the daily number of each. The distribution of inattentive periods appears curvilinear. Inspection suggests that (1) increase in daily number of inattentive periods was associated with a linear decrease in median length per day (slope approximately -1) until number of periods reached 17; and (2) when number of periods per day was greater than 17, median length of inattentive periods per day changed little if at all (remaining at 8–11 min). Median lengths of attentive periods per day, on the other hand, probably continued to decrease linearly as number of periods increased beyond 17, at least to the point of 21 periods per day. An apparent illustration (not graphed) of these relationships is supplied by the female with the exceptionally large number of periods, discussed on page 212. By 1530 she had been away from the nest 29 times, but her median inattentive period still was 6 min long. In contrast her median attentive period had become 11 min, as number of attentive periods decreased (compare 11 min with medians in Table 76).

Length of periods and percentage of attentiveness.—Considering all day-long watches except those on day 1 of the incubation period, no correlation existed between daily percentage of attentiveness and length of the day's median attentive or inattentive periods.

CHAPTER 22

BEHAVIOR DURING THE INCUBATION PERIOD

FEMALE BEHAVIOR AT AND ON NEST

Movement to and from nest.—All females formed habits in selecting routes to and from the nest. No paths were entirely inflexible; an individual might land in the same tree time after time but not on the identical perch, and each sometimes deviated completely. Once at the nest, the same perch was almost invariably used and the nest entered from the same direction.

Speed and directness of the individual's approach also varied. Usually females foraged 50 m or more from the nest, then stopped and flew straight to it; but all sometimes approached slowly (especially in the afternoon), foraging near and even in the nest tree. Before entering the nest most females cast a brief glance into it, but some looked longer and others apparently not at all.

Approaches normally were silent; if the male was nearby or the female alarmed or (apparently) curious she sometimes called Chek or Tsip until reaching the nest, then fell silent. Most (75%) flights from the nest were preceded by an inspection of surroundings. Females then flew 30 m or more before landing (compare Walkinshaw 1953). Although such departures would appear to minimize chances of attracting a predator, all birds sometimes hopped around in the nest tree and its vicinity for 30–60 sec before moving away (compare Mayfield 1960: 96). There was no calling. Departure from nests almost always began with a swoop down to about the level of the forb-grass layer, followed by flight away. Birds on low nests flew away at nest level. The direction taken was highly variable.

Possibly because so much attention for many days was centered on a fixed nest in a relatively unchanging environment, females developed numerous habits associated with goings and comings. Two examples will be described: (1) Immediately after leaving and before returning, a female invariably went to the same blackberry bush among many nearby and ate one or two insects feeding at its flowers. (2) In midmorning of day 1 of incubation, a female landed 4 m from her nest when returning to it. Spying a large insect nearby, she seized it, carried it out of sight, and in 2 min returned and began to incubate. She repeated this behavior at least two more times in the next 4 hours and seemed to be searching for an insect whenever she entered the nest tree; if she found one, she flew away with it. Two days later she behaved somewhat similarly, but now removal of insects was always associated with departure from the nest: She would look around as she incubated, spy a nearby insect, fly out and catch it (once by hawking), and carry it away. The behavior was suggestive of nest sanitation rather than of foraging.

Position while incubating.—The breast was deep, the foreparts apparently lower than the vent with the center of gravity somewhere along the sternum; the tail pointed upward at 45°. Elevation of the head and neck varied. When a

female was nearly asleep or was alarmed, only the upper half of the head and bill were visible at nest level; the bill pointed upward at a slightly lesser angle than the tail. When she was alert, the neck was somewhat extended and the head fully visible, the bill almost horizontal.

Position while standing in nest.—As the commonest response to heat and sun, the incubating female raised her foreparts and sometimes stood. Elevation of the body was at times slight; at maximum elevation the breast was about 1 cm from the inside wall of the nest at its rim. When a female stood, her tail was nearly horizontal, the crissum touching the rim; the tail tilted upward increasingly as she settled into the nest. When I stood over females sitting tamely on the nest, I could see that the feet rested on the cavity floor. By extending the feet and legs the bird could move gradually from an incubating to a standing position with no apparent shifting of the feet; but often the feet did shift. Standing birds occasionally extended the wrists slightly, the primaries parallel to the body; usually the wings were folded.

Females almost invariably opened the bill while standing in the nest. The tips of the mandibles were 1–5 mm apart. Opening was usually gradual, closing quick. The bill was at times left open 4–5 min, more often was opened and closed at least once per minute. In a typical case, during 2 hours when the air temperature was 30°C, a female held her bill open 50–75% of the time.

Birds always first settled on the eggs after returning to the nest; if they stood they did so after 1 min or more. Except at very exposed nests or on extremely hot days, when they might stand 90–95% of an attentive period, females characteristically resumed the incubation position every few minutes, then stood again after 30–60 sec. Alternation of sitting and rising is perhaps a mechanism by which egg temperature is sensed and application of heat regulated (see Lehrman 1961: 1297).

Standing began at about 0830 and was never seen after 1700. Exposure to the sun's rays was not a necessary stimulus for standing and on cool days was not sufficient, but standing began at somewhat lower temperatures if the nest was exposed (compare Lanyon 1958). A female whose nest was fully exposed to sun for long intervals never stood during an all-day observation on a clear, windy day with a maximum temperature of 23°C. Several females on shaded nests began to stand when the temperature reached 28°C. On a hot (27–28°C) afternoon during which the sun shone intermittently, a female repeatedly settled and incubated when clouds covered the sun and stood shortly after the sun emerged, behaving thus even when the nest was in shade; standing may have been a response to slight rises in temperature or to changes in light.

Position while shading from rim.—In shading from the rim, the female gripped the inside of the rim at points not quite 180° apart, flexed her heels (her tarsometatarsi approaching horizontal), and lowered her body and aligned it approximately parallel to the ground. Sometimes her wings sagged slightly and her bill usually opened wide. Such shading was infrequent during incubation, very common after hatching; incubating birds probably shaded only when the temperature was above about 27°C and the nest was in direct sunlight. No female interrupted shading to enter the nest periodically and sit on the eggs, as occurred during standing. If sitting intermittently is a testing of egg temperature, as suggested,

failure to sit during shading may be associated with the higher temperatures usually prevailing during shading.

Direction faced.—Females usually turned on the nest only occasionally during an attentive period. Some invariably faced in the same direction during 1 day; most faced in several directions but evidently preferred one. Choice of direction faced was not associated with my location; some birds faced me, others did not.

Settling prior to incubating.—The female entered the nest and lowered her body; probably after contact was made with the eggs, she rocked her body, especially the posterior half, from side to side about 10 times. Occasionally the legs were seen to move, evidently kicking; the feet were probably sometimes used to turn the eggs or bring them into position against the incubation patch (compare Harding 1931). Settling occurred after returning to the nest to incubate, also after rising (below) and resuming incubation.

Rising; inspecting nest contents.—Incubating females (except when leaving the nest) rose by standing and backing away from the wall in front of them. When leaving the nest, they jumped quickly to the rim in front or to one side. After rising, birds often moved the head forward and downward, frequently turned slightly to one side, and looked into the nest.

Removing invertebrates; touching eggs.—Judging from the fact that the bill moved as in eating, sometimes females rose to remove invertebrates from the nest. (They certainly did so when the nest contained nestlings; see pp. 278–279.) Contact between bill and eggs could not be observed, but deep probing into the cavity was common and doubtless often turned and rearranged eggs; most probes were brief (1–30 sec, rarely more than 5 sec) and probably shifted the eggs only slightly.

Manipulating nest material during incubation.—Incubating females occasionally rearranged fibers on the nest rim or the outer surface, in the latter case leaning out forward or sideward. Sometimes birds tugged very vigorously at objects in the cavity; probably only nest material would offer sufficient resistance to cause such tugging.

Entering nest when disturbed.—Several times females perching on the rim or standing in the nest settled quickly at my approach or that of birds or small mammals. Perhaps related were what looked like false starts to leave the nest; an incubating bird would jump to the rim, crouch for flight, but instead quickly re-enter and sit.

Scanning surroundings prior to leaving nest.—Most females became noticeably more watchful 0.5–3 min before leaving the nest, turning the head horizontally and scanning the entire 360°; sometimes (especially when on high nests) they craned the neck and surveyed the ground below. At times incubating females facing away from me glanced back to look at me just before leaving (compare Cox 1960: 18).

Extending and retracting neck during incubation.—Birds deep in the nest with head retracted responded to certain noises by quickly extending the neck upward to its full length, then pulling it down again so gradually and smoothly that movement was barely detectable. (Compare the gradual submergence of grebes.) This may have been a response to unidentified or puzzling sounds; it was

observed when females evidently heard a falling leaf, a bird landing nearby, a Yellow-breasted Chat calling. Noises that I made during long watches elicited it.

A female in whose vicinity Blue Jays foraged pulled in her neck quickly instead of extending it and also ducked when jays called without warning. Possibly this movement was reserved for familiar noises associated with danger. Sturm (1945) reports similar behavior in incubating American Redstarts in response to the presence of cowbirds and Common Grackles.

Shaping nest during incubation.—One incubating female engaged briefly in nest-shaping movements, thrusting her wrists against the inner walls in the manner of building birds (Chapter 16).

Frequency of moving eggs during incubation.—The cumulative effect of the foregoing activities (especially probing, foot movements, and settling) probably was gradually to rearrange the position of the eggs; marked eggs changed positions from day to day. I could detect little tendency for the frequency of the movements to vary according to time of day, except that most shifts resulting from responses to heat were in the middle of the day, and those caused by settling after inattentive periods paralleled rhythms in attentive-inattentive behavior (Chapter 21). Shifting of eggs apparently did not occur more or less often as incubation progressed, but when hatching began females poked at eggs very frequently (see p. 242). Examples from the middle of the incubation period will illustrate the frequency of acts that probably moved eggs: (1) A female that spent 344 min on the nest between 0524 and 1311 (total period 467 min) probed and settled 24 times; rose, looked into the nest, and settled 3 times; settled after returning to the nest 12 times. Thus she probably moved eggs 39 times, or about 8 times per hour. (2) A female under observation all day probably shifted her eggs about once during each of 25 attentive periods; she settled after each inattentive period, therefore probably moved her eggs only about 50 times during about 15 daylight hours. (3) A female probably moved her eggs only 4 times in the first 3 hours of daylight on 1 day; during that 3-hour period 4 days later she probably made 5 egg movements.

Preening.—Preening was common; especially at high temperatures, females often preened repeatedly and long (compare Franks 1967), using all normal movements (see Chapter 40) except those directed at primaries. Usually they preened while standing, behavior also associated with heat; occasionally the back, scapulars, and upper breast were preened while the female was sitting.

Dozing.—Dozing probably was associated with drowsiness (but see Franks 1967) and was commonest in the morning; 15 of 21 observations were before 1000, 2 shortly before nightfall. (Repeated dozing in a single brief period is counted as one case; dozing usually occurred in a series of repeated acts.) Behavior took two forms: (1) turning the head toward the rear in the approximate position of a sleeping bird, but without tucking the bill into the scapulars; and (2) closing the eyes, head facing forward and neck retracted. The eyes usually closed slowly and opened suddenly 5–19 sec later, as though the bird were fighting to stay awake. Once a female dozed while standing in the nest on a hot day.

Watching and catching insects.—Females often watched crawling or flying insects and sometimes reached out and caught and ate them. Occasionally a bird left the nest 1–2 m to grab an insect, then quickly returned.

Miscellaneous acts.—At times females opened the bill and immediately closed

it, apparently yawning. Twice a bird got to the rim, shook her wings and body as after bathing (see Chapter 40); this occurred on a warm dry afternoon. Once or twice incubating females stretched both wings upward while sitting; birds on the nest rim engaged in all normal forms of stretching (see Chapter 40).

Reactions to intruders near nest.—Except for distraction displays, which were rare until the eggs hatched and are described in Chapter 25, reactions to intruders during the incubation period and the nestling interval were about the same. Where there were no differences, observations from both stages are included here. In describing certain experiments, reactions of males are included.

Prairie Warblers: Agonistic behavior by the female toward her mate was very rare. Twice females turned on mates following them to the nest; one gaped, and the other darted at the male 7 m from the nest and drove him away. Females usually appeared indifferent toward males that were not their mates. Incubating birds watched such males from the nest; females returning to the nest and meeting a strange male or neighbor ordinarily sat quietly, tail bobbing nervously, until the male left. Once (in about 25 observed meetings) a female supplanted a male attempting to go toward the nest with her. Another, unmated female (deserted by her mate) appeared to solicit copulation from an exploring male (see Chapter 30; see also pp. 106–108); this occurred in the nest tree. All characteristic precopulatory behavior was observed, but the female also opened her upward-pointed bill (gaped?).

Visits of females to nests of other females were observed three times; reactions of nest owners were dissimilar. (1) While I watched incubation by one of a polygynous male's two mates, the other (probably—she was not banded) came to the nest, approached the incubating bird within 10–20 cm and looked at her; neither female postured. The visitor moved away, returned, and looked at the incubating bird, which turned her head and faced in the other direction (compare p. 45). This episode lasted 2 min. (2) Two days later the same (?) female again approached this nest and perched 20 sec almost on its rim; the females simply looked at each other. (3) A female whose nest I was watching all day fought another female intermittently for 7 min. The incubating bird started the fight by leaving the nest and chasing the approaching intruder. Loud Cheks and Squeaks were uttered, as in some male fights. The nest owner then supplanted and drove the intruder, perched with retracted neck, gaping, wings out (see Chapter 7). The intruder fanned her tail quickly several times in a tail spread, elevating it to 45°. Two more supplantings by the nest owner were accompanied by bursts of Cheks and Squeaks. The intruder then raised the crown feathers while sitting stiffly, watching the nest owner. Two other encounters followed, but vegetation prevented close observation. One Whine was heard.

Once a 44-day-old member of a first brood accompanied the female to her second-brood nest after an inattentive period; it hopped around just below the nest, jumped up to look at the incubating female from a distance of 8 cm, and left after 20 sec. The female ignored the young bird.

Other small birds: Prairie Warblers and Field Sparrows were often near each other and occasionally appeared curious about each other (see p. 58). Six times incubating warblers ignored Field Sparrows in the warblers' nest trees, even when the sparrows were very close. However, two females repeatedly flew

at and drove Field Sparrows away; two immature sparrows were involved in one of these cases, and each time the warbler chased one sparrow the other would fly to the nest and look in at the nestlings. Three incubating warblers that were approached by sparrows watched quietly until the sparrows flew, then chased or followed them; one of these females had risen and stood in the nest when the sparrow approached. One female, foraging near her nest tree, permitted a Field Sparrow to go to her nest; she perched nearby and watched the sparrow.

A female flew from a nest containing young when a female Indigo Bunting entered the tree; two females ignored buntings near the nest. A fourth left the nest and perched beside it to watch a male bunting below her; when the bunting was within 0.5 m, the female hopped toward him and gaped; the bunting left.

Other small birds evoked few aggressive responses, even when very near warbler nests. Ignored were Blue-gray Gnatcatcher (5 times); Carolina Chickadee and American Goldfinch (3 times each); Worm-eating Warbler, Red-eyed Vireo, and a brood of Common Yellowthroats (1 time each). Occasionally birds of those species were chased or caused incubating warblers to stand and watch them attentively or to gape. Only once did a female perform distraction display, suggesting that small birds inspired little fear.

Only one female left the nest to attack a larger bird; this warbler, whose eggs had just hatched, turned toward a Yellow-breasted Chat that landed by the nest, extended her wrists, thrust her head forward, and probably gaped; the chat flew and the female chased or followed. Another female (just after laying an egg) did not react overtly to a chat that sat almost on the nest rim and looked at her for 2 min. Female Cardinals, a female Scarlet Tanager, and a Tufted Titmouse near nests were closely watched by incubating warblers. Walkinshaw (1959) reports that a female Prairie Warbler "scolded" Common Crows in trees overhead.

Mammals: Agonistic reactions toward mammals were not observed, except toward man. Rabbits near low nests were ignored after an initial glance. Twice barking dogs about 20 m from nests elicited no reaction. A female built a nest 2 m above the ground, 5 m from a Red Fox den; the fox cubs frequently sunned and played near the nest but were ignored by the warblers; the nest succeeded.

Reactions to me varied greatly. Some females appeared indifferent or soon became so. One bird I visited often had to be pushed off the nest (in 2 years) before its contents could be examined; she snapped and bit at a mirror on a stick, retreating grudgingly to the nest rim. (Walkinshaw 1959 and Lovell 1949 picked up females from nests.) At the opposite extreme, some females jumped from the nest when I was still 20 m away; one did this although her nest was 8 m above the ground. The commonest responses were intermediate: females usually left the nest when I was 2–3 m away, retreated a short distance, and called Tsip or Chek. Birds returning to the nest and finding me there called and hopped around or perched near me; if I sat or was motionless most went to the nest and quit calling. Occasional reactions of incubating females to me were distraction display (five cases), gaping (two cases), cryptic entering of the nest, and zooming (see p. 501). Note that gaping had been fairly common during building (see p. 143), became uncommon during incubation, and was never seen after the eggs hatched (when distraction display became the usual response). In the case of zooming, a female that had gone to the nest to lay her final egg saw me sitting 15–20 m away; she

flew straight at my head, veering off at the last minute and passing so close that I could hear her wing beats.

Dangers probably from overhead: Several females (and, during the nestling interval, males) on or at the nest froze, i.e. stood motionless; a Broad-winged Hawk flew over during one instance. The position of the body was the same as in tense crouching (Chapter 7); the plumage may have been somewhat sleeked; the head sometimes was thrust forward with the bill horizontal, but at other times the neck was retracted and the bill pointed upward at about 45° (compare Mayfield 1960: 63). Experiences with helpless Prairie Warblers suggest that freezing may be a response to danger from above. Young birds near the ground sometimes froze as I stood over them (but this may have been a reaction to Tsip calls of adults). An injured female when released fluttered into a dense clump of forbs and grasses and froze for 5–10 min.

Experimentally introduced mounted specimens: A mounted male Prairie Warbler placed near nests caused the male parent to hover above and in front of it, then to perch nearby with tail bobbing nervously. Females gave little or no observable reaction.

A mounted female Brown-headed Cowbird was placed near nests containing eggs and nestlings; adults were absent when the skin was introduced. Two females with eggs hopped and flew nervously around the mount; one Sputtered when she first saw it, and both gaped and called Tsip every 1–2 sec. Neither would go to nest until I removed the cowbird, after 15 and 25 min, respectively. A male and female with young 5 days old behaved about as described, except that both flew at the mount and hovered 1–2 sec some 30 cm from it; one then flew at and hit it. Finally both perched and hopped 2–3 m from it, calling Tsip frequently for 7 min, after which I removed the mount.

Believing chipmunks to be important predators on eggs and nestlings (see p. 415), I twice placed a mounted chipmunk 50 cm from nests containing nestlings. Both females went to the nests, and one gaped for 30 sec. No other behavior directed toward the mount was observed.

FEMALE BEHAVIOR AWAY FROM NEST

Behavior at dawn.—A female's first act after leaving the nest at dawn was to preen thoroughly for 4 min, perched 20 m from the nest. Walkinshaw (1959) saw a female catch food and eat immediately after leaving the nest for the first time.

Foraging behavior.—Although females sometimes foraged slowly, particularly in the afternoon when inattentive periods were longer (Chapter 21), most foraging during incubation and the nestling interval was unusually rapid, with darting movements and many short flights (compare Sturm 1945). Their pace was approximately twice as fast as during the egg-laying interval or after reproduction. This rapid movement presumably was associated with the short time available for feeding (see also Chapter 39).

Behavior while leaving territory.—Occasionally females ignored boundaries and foraged on adjacent territories. When noticed by territory owners they were courted or followed, sometimes back to the nest. Females accompanied by their mates during inattentive periods did not leave the territory (only one exception).

Relations with mate.—Behavior in this category is described in the following section.

MALE BEHAVIOR

Singing.—Song is discussed in Chapter 8, with considerable emphasis on the incubation period, when singing was more frequent than during any other stage of the pair's association.

Males usually sang less frequently when females were off the nest than when they were on it. During seven day-long watches (involving four males), I recorded numbers of songs during all female attentive and inattentive periods. When numbers of male songs and of female minutes on and off the nest are tested for goodness of fit, very large Chi-square values (26.7–156.2) are obtained for 5 of the 7 days. For example, a male sang 793 songs during a day lasting 915 min; the female was off the nest for 318 min, in which he sang 178 times instead of 276 times expected under the null hypothesis. Nor was this reduced singing simply the combined result of tendencies of males to sing less in the afternoon (Table 12) and of females to be less attentive at that time (Fig. 18): The male just referred to sang 502 songs during 445 min between his first song of the day and 1230; the female was off the nest 173 min of this period; in this time the male sang 118 times; adj. Chi-square = 49.3.

On two of the seven all-day watches song was not significantly less frequent when females were inattentive. To attempt an interpretation of these conflicting results: On most days females probably joined their mates during parts of their inattentive periods, and the males usually followed them in silence. Males began to sing as soon as the females returned to the nest. The fact that on some days song was unabated during inattentive periods may have been the result of failure to join the male as often on such days. A female might be less inclined to seek out her mate on some days than on others; within a single day she sometimes left the nest and flew toward the place where the male was singing and sometimes did not.

Causing female to leave nest.—Males did not approach the nest and "call the female off," as males are said to do in some species. Sometimes females did leave the nest just after a song, probably terminating an attentive period that had already about expired. An unusual episode is consistent with the suggestion that only when the female's motivation to incubate was low did she respond to singing by leaving the nest: The bird that deserted late in the afternoon of an all-day nest watch (see p. 212) ended her morning attentive periods without apparent regard for the male's singing. The first sign that she might desert was that in midafternoon she began to leave the nest whenever he sang, even if she had been incubating only a few minutes. She rose at the beginning of a song series and after one or two songs often flew toward the singer.

Accompanying female.—As stated, during female inattentive periods the male at times accompanied her, staying within 3–20 m and watching her intently and usually silently (compare Walkinshaw 1959). An occasional male sang very softly, and others sang a few songs at normal volume.

During 21 long watches (see Chapter 21) at nests of incubating, mated females

I saw the male accompany the female to or almost to the nest only 14 times (earliest 0629 and latest 2020); no male did so more than twice during a watch. Distribution of cases according to hour was random, and this appeared to be true throughout the incubation period. Many cases were observed in addition to those during long nest watches; some males interrupted tending of first broods to join mates and go to the second-brood nest with them. Males accompanying a female landed in the nest tree about when the female did and usually left almost immediately after she settled; rarely a male went to and looked into the nest before his mate entered. One sang a quiet Chatter from the rim. In an unusual episode on day 1 of the incubation period of a first nest, a male got into the nest while the female perched just beneath it. He sat deep in the cavity for 6 sec, during which his legs moved as though kicking the eggs (compare Mayfield 1960: 97).

Sexual behavior.—Emlen states (1955: 114) that after the onset of incubation “[s]exual behavior is completely suspended in most species . . .” (see also Emlen 1941, Lehrman 1961: 1271–1272). As indicated in Table 26, the Prairie Warbler is an exception to this statement. A male copulated with a female returning to her nest to resume incubation. Another, tending fledglings of the first brood, lit on the back of his mate while she was absent from her second-brood nest; they appeared to copulate. When he left her back, the female solicited copulation; he approached again but she repelled him. They then moved along together briefly and copulated once more. Other cases of sexual behavior also occurred during the incubation period.

Anticipatory food-bringing.—Males visited nests alone, doing so without respect to whether the female was present; on 76% of these male visits the female was on the nest, which corresponds roughly to the percentage of daylight attentive time of females (see Chapter 21). Of 56 observed visits, males arrived with food 45 times, without food 3 times; 8 times I could not be sure whether food was brought. (The unusual case described on p. 195 is not included in this discussion.)

An earlier paper (Nolan 1958) analyzed the data then available and attempted to relate the Prairie Warbler's behavior to food-carrying by other male parulids. This section brings the data up to date and modifies two earlier statements. Discussion will not be repeated except to state that I suggested taking food to the nest during incubation functioned principally to acquaint the male with the fact that the eggs had hatched. Skutch (1953: 10) had earlier proposed this view and used the term “anticipatory food-bringing,” which I adopted with no anthropomorphic intent (see Berger 1961: 257).

Trips without food were too few to be analyzed; only food-bringing will be discussed. Twenty-four males engaged in the behavior, in all normal weather including during rainfall. Ages of six were known: all were older than 1 year. But no male whose nest was watched for 1 or more days failed to carry food at least once (except a male caring for first-brood fledglings while his mate incubated), and 35% of all males were yearlings (Chapter 38); therefore some food carriers probably were yearlings.

Reactions of females, when present: Sixteen times when the female was present I could see her behavior; 7 times she took the food and ate it; the male ate it 3 times, carried it away 4 times, and twice disposed of it in a manner I could not see. Most females seemed to ignore males, even to turn the head away;

most males did not appear to thrust the food toward the female's mouth. Females that took food did so only after males had been present for several seconds.

Frequency and timing of food-bringing: To determine number of food-bringing trips per day, I used 21 long watches at nests of mated females; the pairs had no first-brood fledglings. On 1 day the male carried food 3 times, on 5 days 2 times, on 9 days once, and on 6 days not at all.

Trips were distributed during the day about as were trips to feed nestlings (see Chapter 24). The earliest was at 0615 and the latest at 2015; of the 45 observations, 31 were made before 1130, about evenly divided among morning hours.

Whether individuals were consistent in the timing of trips from day to day is not clear. One bird's first trip on each of 3 different days was at 0749, 0635, and 0751; but on another day (day 7 of incubation) he did not go to the nest at all. A second male's first visits on 4 different days were at 0615, 0626, 0634, and 1422. A third male's first trips on 3 days were at 0705, 1824, and at 0639.

Twice I saw males take food to the nest on the day before egg 1 was laid, another on the day before the final egg was laid (see also p. 195). Three males made food trips to nests that had already failed (5, 27, and 36 hours previously; compare Welty 1962: 166). In one of these cases, the male was unmated, his mate having disappeared 1 day earlier.

Day-long watches suggest that anticipatory food-bringing was more frequent at the end than the beginning of incubation, a view inconsistent with that expressed in my 1958 paper. During 4 of 7 watches on day 1, males did not bring food; as noted above, on only 6 day-long watches was the behavior omitted. The one male that made 3 trips did so on the last day of incubation; on 3 other nest watches on the last day, I saw 2 trips twice and 1 trip once.

The earliest observation was on 26 May, the latest on 22 July. Long watches were not uniformly distributed in date, and variation with date is not certain. However, during 7 all-day watches of first nests, anticipatory food-bringing occurred on 2 days and was omitted on 5. The distribution of 17 chance observations of food-bringing also suggests variation: 2 were 1–15 June, 7 were 16–30 June, and 8 were in July. The number of males with incubating females was largest in May and least in July (see Chapters 31, 33, and 34), so it appears that the likelihood a male would take food to the nest increased as the season advanced.

In the earlier paper I erroneously stated (1958b) that nine males had had no earlier nests in the season in which they engaged in anticipatory food-bringing. I should have said no earlier nests in which eggs had hatched.

Other male food-bringing behavior.—I once took a fledgling from its parents to use to lure a distant male into a net. To prevent the fledgling from calling while I put up the net, I covered its cage with a tarpaulin. Despite this the young begged. The territorial male, whose mate was incubating, instantly flew to within 15 m of the tarpaulin and appeared to look in its direction. He then caught a caterpillar and flew with it toward the nest. I did not get to the nest in time to see whether he went to it.

Miscellaneous behavior.—Accompanying the female to the nest was less frequent than food-bringing and rarely acquainted the male with the situation in the nest,

because he seldom examined the nest's contents. Even when males did see their new young as the result of accompanying the female, I observed at least one and possibly two cases in which they did not begin to feed for at least several hours.

The male did almost nothing resembling guarding the nest while the female was away (compare Mendall 1937, Pitelka 1940, Walkinshaw 1953), except occasionally to approach me and show mild alarm by calling and bobbing the tail (see Walkinshaw 1959). Once while a female cowbird was in the nest tree, the male called in a nearby bush; the cowbird soon left, and the warbler flew into the nest tree.

Males whose mates were incubating probably often left the territory to wander over surrounding areas, as described in Chapter 30. Compare Kendeigh's statement (1945: 155–156) that during the incubation period the male Chestnut-sided Warbler "greatly extends the area over which he roams, going well outside his previous territorial boundaries."

EXPERIMENTS: FEMALE REACTIONS

In about 70 instances in addition to those described in other chapters I changed contents of nests or introduced fledglings near nests being incubated or brooded. My objectives were often to facilitate capture and banding of adult warblers, but I also obtained information about parental behavior. My results resemble those of Emlen (1941) for Tricolored Redwings and indicate that the Prairie Warbler is another of possibly a limited number of species (see Lehrman 1961: 1302–1304) in which incubation and brooding are interchangeable. Experiments with incubating females and females caring for nestlings cannot be separated conveniently and will be reported together.

Incubation of eggs of other species.—Field Sparrow eggs were introduced in substitution for warbler eggs, which they resemble closely, and were accepted in all cases (15). Indigo Bunting eggs, pure white and slightly larger than warbler eggs, were substituted once and accepted and incubated for 10 days, until they hatched.

Prolongation of incubation.—Once I replaced well incubated warbler eggs with fresh warbler eggs, another time with fresh Indigo Bunting eggs. One female warbler incubated a total of 20 days (beginning with the day she laid the final egg) and deserted just before the substituted (living) eggs would have hatched (compare Hofslund 1959: 164, Mayfield 1960: 92–93). The other female incubated 18 days; the Indigo Bunting eggs then hatched.

Abbreviation of incubation.—Introduction of nestlings during the incubation period regularly caused female warblers to abbreviate, even to omit, that period. In nests containing eggs I put nestling Prairie Warblers 13 times, Field Sparrows 17 times, Indigo Buntings 3 times, Chipping Sparrows 3 times, cowbirds 2 times. Usually I added one nestling, sometimes two; rarely I removed the warbler eggs from the nest.

One female warbler deserted a 4-day-old Field Sparrow immediately after its insertion, but all other introduced nestlings were accepted and promptly fed. Ten females that fed nestlings did so on day 1 of the incubation period; 13 others fed young introduced on day 2. Yearling and older females did not

differ. Most nests were the first of the season, but some were built in June and July. Introduced nestlings were 1–7 days old. In the few observed cases, the reaction of females that returned from an inattentive period and discovered the introduced young was to look into the nest about 30 sec, to brood about 5 min, then to leave and obtain food. Thus feeding took place within about 10 min (minimum 7 min) of the finding of the young.

The greatest abbreviation of the nesting cycle was at a nest in which a female laid her final egg and accepted a large nestling warbler on 3 July, continuing to give the nestling full attention until (and after) it left the nest on 6 July. The interval between beginning of building and nest-leaving was reduced from the norm, about 28 days, to about 10 days.

Unless later removed by me or a predator, young were tended until they left the nest, all in apparently normal condition. Introduced Prairie Warblers were reared to independence; two females that brought off introduced young at early dates attempted second broods. More interestingly, two introduced Field Sparrows among three that left the nest were tended until probably independent, as will be described: (1) A young sparrow left on 31 May and was still being fed by both foster parents on 16 June. The female probably then began a second-brood nest; the male was still feeding the 32-day-old sparrow on 22 June. (2) A sparrow left a warbler nest on 7 June; the female continued to sit on the nest (which still contained her eggs) until at least 10 June, while the male cared for the sparrow. On 10 June, the sparrow persistently followed and begged from a female American Goldfinch, whose colors somewhat resemble a Prairie Warbler's. I last saw the sparrow on 15 June, when both warblers fed it, the female directing a distraction display at me. She also drove adult Field Sparrows away from her foster fledgling; other details were not observed, but the sparrows were perhaps attracted by the fledgling's frequent calls.

One Field Sparrow and two Chipping Sparrows left (three) nests at the normal age and were never seen again; they probably were ignored by the warblers and allowed to die. A young cowbird remained in a nest from which one of the Chipping Sparrows fledged, and the cowbird continued to be tended by the warblers. A male Prairie Warbler that had a foster-fledgling Chipping Sparrow was polygynous; he appeared to devote himself solely to warblers in the nest of his second mate.

Resumption of incubation.—From 13 nests I removed nestlings that I had introduced and that had been accepted by the adults; Prairie Warbler eggs, which I had not removed, remained in all 13. Ten female warblers resumed incubation, two did not, and one probably did not. I believe those that did not had seen me remove the nestlings, but some females that saw me did resume. My removals produced a situation like one that occurred in nature when predators took newly hatched young from nests on hatching day and left live, unhatched eggs; in such cases some female warblers deserted the remaining eggs, but most did not (see p. 388). The longest period during which a female had cared for young before resuming incubation was 101 hours; another period was 53 hours, and several were 30–50 hours. Desertion, as opposed to resumption of incubation, was not associated with length of the period the female had fed the young before their removal. Efforts to watch females' reactions when

they returned with food and found only eggs were unsuccessful; I could not distinguish agitation toward me from behavior caused by absence of the young. The time required to revert to incubation is unknown; but some or all eggs hatched in all nests that escaped predation, so the period probably was brief.

Neither the species of substituted and subsequently removed nestling nor its age (4–8 days) when removed seemed to affect whether the female deserted. An important factor was whether I had hoop-netted the female at the nest and, if so, the period between such netting and my removal of the young; the shorter this period, the more likely was desertion. Sometimes I took the nestling 48 hours after netting females, but usually about 24 hours afterward. Twice I removed it at the time I caught the female, and even one of these females resumed incubation.

Response to alteration of nestling interval.—Introduced nestlings often left the nest at the normal age, but from the point of view of the foster parents the nestling interval was abbreviated by 1–6 days. Nevertheless, with the exception of the cases mentioned above (note that all involved young of other species) female warblers immediately transferred full attention from their own eggs and nests to the foster fledglings.

Three cases suggest that the nestling interval can be prolonged artificially. In two, young warblers were put in nests containing well incubated eggs. The females' own eggs hatched 24–48 hr after introduction of the nestlings, and I then removed these foster young; the females fed their own young until the nests were destroyed by predators. In the third case I took all young, 9 days old, from a nest and put them in a cage nearby, where they died of heat. I then put a brood of 5-day-old warbler nestlings in the cage, and the mother of the dead nestlings fed these through the mesh until nightfall. Next day I put these foster nestlings back in the female's nest, 28 hours after I had removed her own young. She fed the nestlings, which left the nest at the normal age and were tended until independent.

Reaction to fledglings introduced near nest.—I introduced fledgling Prairie Warblers into the vicinity of nests of three incubating or brooding females, whose reactions differed considerably. One female no longer had a mate; on day 5 of incubation she stayed on her nest at least 5 min while the caged fledglings begged, but within 10 min she was attempting to feed them, exhibiting alarm toward me (Tsip and Sutter calls) but giving no distraction display. An incubating female probably never (during 2 days) fed two fledglings liberated below her nest, but her mate fostered them. A female with nestlings directed distraction display at me when two introduced fledglings called below her nest. Later, the fledglings attracted her attention and diverted her when she started toward the nest carrying food; she seemed unable to choose between her nestlings and the fledglings. I removed the caged birds, not having seen her feed them.

EXPERIMENTS: MALE REACTIONS

Feeding nestlings.—Males fed foster nestlings about as soon as they fed their own young after eggs hatched (see p. 259). In two exceptional cases, males accompanied females to the nest and may have seen the introduced young.

One brought food after 17 min, the other after 30 min. These could have been cases of anticipatory food-bringing, but their timing so soon after the males' visit suggests a causal relationship.

In contrast, another male followed his mate to the nest repeatedly as she took food to an introduced nestling; he looked at or into the nest four times in 40 min but brought no food. Four hours later he was feeding.

Reactions to fledglings.—Whenever any fledgling I was carrying called, the owner of the territory on which I happened to be quickly approached and called Chek. If I put a caged fledgling down, the male usually showed interest for at least 1–2 min and sometimes brought food. Four males left the vicinity of the cage and did not return but probably had not seen the young.

In the only case in which I liberated fledglings on the territory of a male that did not have young of his own he took over their care. Once I put two caged young below a nest containing nestlings. The male approaching with food heard the calls of the introduced young and flew toward the cage, at first showing no excitement or alarm at me. The caged young saw the male and began to beg, evidently causing him to see them. He performed very intense distraction display and later fed them.

CHAPTER 23

DURATION OF INCUBATION; HATCHING

LENGTH OF INCUBATION PERIOD

The incubation period is measured in hours from the laying of the final egg until its hatching, using only data from nests in which that egg was marked. Because of heavy nest predation and cowbird interference (Chapters 32 and 33) there are only 43 cases. The periods' beginning can be fixed with considerable precision; several layings were observed, and in the remaining instances laying can be assumed to have been at about 0600 (Chapter 20). Five times of hatching of the final egg are known. In all other cases hatching fell between 2 nest inspections; intervals between inspections were 1–5 hours in 8 cases, 5–12 hours in 18, 12–24 hours in 11, and 30 hours in 1. In these cases the incubation period is taken as having ended midway between the two inspections, with a margin of error of one-half the interval separating inspections. Margins of error are rounded to the nearest half hour and are shown following the letters "m.e." When incubation periods are arrayed from shortest to longest, those with large and those with small margins of error are about evenly distributed along the array. In cases in which hatching was not observed, the mean margin of error was about 6 hours, which is used as the mean for the full sample. In calculating standard deviations, margins of error were ignored.

The longest incubation period lasted 345 hours (m.e. 2.5 hours), or about 14.5 days; the shortest was 249 hours (m.e. 4.5 hours), or about 10.5 days; the mean of 43 cases, rounded to the nearest hour, was 287 hours, or 12 days (SD 18 hours, m.e. 6 hours). As will be seen (Table 77), 37% of the cases fell in the modal 5-hour unit interval of 280–284 hours, or 11.5–12 days. Included in the sample are five periods that were probably prolonged (see below) because of the presence of cowbirds' eggs and, later, nestlings. The mean length of 38 periods not potentially affected by cowbirds was 285 hours (SD 16 hours, m.e. 6 hours).

The lengths of two incubation periods for which there was no error (I watched both laying and hatching of the final egg) were, respectively, 289 hours 27 min and 292 hours 47 min. In 3 instances I did not watch laying but did observe hatching, and the margin of error therefore probably was negligible; lengths of these periods were about 274, 291, and 294 hours. One incubation period was measured in an incubator; an egg inserted immediately after laying and kept at 37°C and a relative humidity of about 50% hatched 286 hours (m.e. 1.5 hours) later.

Disregarding margins of error, the longest incubation period was 39% greater than the shortest, which in turn was 22 hours shorter than the next shortest case. Nice's (1953) research indicates that a period of 249 hours is rare for any passerine, and this is clearly true of the Prairie Warbler: In addition to the 42 full periods longer than 249 hours were 10 others at nests that failed before

TABLE 77
LENGTH OF 43 INCUBATION PERIODS¹

Length, hours	Number
248-269 ²	1
270-274	7
275-279	1
280-284	16
285-289	5
290-294	5
295-299	3
300-345 ³	5
Total ⁴	43
Mean, all cases	287 (SD 18 ⁵)
Mean, 38 cases not involving cowbirds	285 (SD 16 ⁵)

¹ The incubation period is measured from laying to hatching of the final egg. See page 235 for additional methods.

² The case in this interval was a period of 249 hours (m.e. 4.5 hours).

³ These were periods of 308 hours (m.e. 6.0 hours), 309 hours (m.e. 7.0 hours), 317 hours (m.e. 1.5 hours), 331 hours (m.e. 5.5 hours), and 345 hours (m.e. 2.5 hours).

⁴ Included are five incubation periods that were probably prolonged because nests contained one or more cowbird eggs. Lengths were 317 hours (m.e. 1.5 hours), 308 hours (m.e. 6 hours), 296 hours (m.e. 1.0 hours), 291 hours (m.e. 1.0 hours), and about 291 hours.

⁵ As discussed on page 235, means, rounded to the nearest hour, are subject to a margin of error of about 6 hours. Standard deviations were calculated without considering the individual or mean margins of error.

hatching began but after more than 250 hours of the incubation period had elapsed.

Walkinshaw (1959) obtained some evidence that two clutches in Michigan took about 12 days to hatch; a third clutch had an incubation period of about 13 days. A number of earlier writers (e.g. Daniel 1901, Baerg 1931: 144-145) report a 14-day incubation period but do not describe their methods of measuring it.

Variation with air temperature and date.—Cool weather prolonged the incubation period. The longest periods, 345 hours (m.e. 2.5 hours) and 331 hours (m.e. 5.5 hours), were observed at two contemporaneous nests incubated for about 14 days; during the period the average daily mean air temperature was 15°C. In both these nests, the final egg was laid 9 May 1960, when the mean temperature was 6.7°C; next day the mean was 4°C, and the weather remained cold until 14 May. The two females were not found on the nest during several inspections on 9 May, and only one was found incubating on several inspections on 10 May. As described elsewhere (pp. 156, 185), during this cold spell there were also departures from normal behavior in both nest building and egg-laying. During the 11 days when the shortest (249-hour) incubation period occurred the average daily mean temperature was 26°C.

That avian embryonic development is retarded at low temperatures and accelerated at high is generally established (see Rol'nik 1970: 296-297). At least two factors probably combine to produce this cool-weather effect in the Prairie Warbler. (1) Eggs presumably cool faster during inattentive periods; even during attentive periods, they may be cooler than eggs incubated in warm weather. (2) As indicated above, females appear to incubate less (see also Chapter 21).

TABLE 78
LENGTH¹ OF INCUBATION PERIODS,² ACCORDING TO DATE³

Incubation periods	9-19 May	20-31 May	June	July
N ⁴	14	11	11	7
Extremes	345-278	296-274	291-271	285-249
Mean	299	285	282	276
m.e. ⁵	5.5	5.5	4.5	6.5
SD	20.7	8.3	6.7	14.1

¹ Lengths are in hours.

² The incubation period is measured from laying to hatching of the final egg. See page 235 for additional methods.

³ Periods are assigned to dates on which they began.

⁴ Included are 5 incubation periods that were probably prolonged because nests contained 1 or more cow-bird eggs; see page 238. One fell in the interval 9-19 May, 2 in 20-31 May, and 2 in June.

⁵ m.e. = margin of error, which is half the time separating the two nest inspections between which the final egg hatched.

A greater percentage of time was spent in incubation as the date advanced (see Chapter 21), a change probably partly independent of weather. That a decrease in incubating time prolonged the incubation period, even in warm June and July weather, was indicated by experiments in which nestlings were introduced into nests. Two examples will be cited. (1) A nestling was put into a nest on day 1 of the incubation period (14 June) and removed 4 days later. The female spent less than the normal time incubating during the 4 days in which the young was present, often leaving the nest to get food for it. Air temperatures were normally warm. The incubation period was very long, about 330 hours. (2) A female left the nest often to feed a nestling introduced on day 2 of the incubation period and removed 2 days later (6-8 July). Air temperatures were high (to 32.2°C). The incubation period was about 305 hours, i.e. 20 hours longer than the July maximum (Table 78). The increase in these two cases may have been attributable in part to the nestling's interference with contact between incubation patch and eggs. In any event, even in the warmest part of the breeding season the incubation period's duration apparently was affected by the proportion of time heat was applied to the eggs during the daylight hours.

Table 78 presents period lengths during four calendar intervals, according to date of day 1 of the incubation period. May is divided into two parts of about equal length; the other two intervals are June and July, respectively. Inequality in length of calendar intervals was accepted in order to avoid excessive disparity in sizes of samples. In an analysis of variance in which margins of error were ignored, $F = 4.47$; $df = 3$ and 39 ; $P < 0.01$. The mean for the early-May interval differs from all other means, which are homogeneous (Student-Newman-Keuls test). When margins of error are considered, it will be noted (Table 78) that differences between mean incubation periods of any 2 of the last 3 calendar intervals are smaller than the combined margins of error of the same 2 intervals; on the other hand the difference between the mean period for 9-19 May and the mean period for any other calendar interval is larger than the 2 margins of error combined.

Despite their statistical homogeneity, mean periods for the final three calendar intervals suggest a progressive shortening as the date advanced. Even if the unusually short period of 249 hours is omitted from the July subsample, the mean

length of the 6 remaining July periods is 281 hours, which is shorter than the mean length of any other interval. Note also that extreme lengths diminished steadily from one interval to another. This probable seasonal reduction may have been largely attributable to steadily increasing air temperature during the breeding season. As a conjecture, eggs in first nests may also have taken longer to hatch because the female's incubation patch, which was incompletely defeathered during the laying of first clutches (pp. 195–196), may not always have been fully functional when the incubation period began.

Variation because of cowbird parasitism.—Five incubation periods at nests that cowbirds had parasitized suggest that parasitism slowed down development of warbler eggs. Lengths of these periods were 317 hours (m.e. 1.5 hours), 308 hours (m.e. 6 hours), 296 hours (m.e. 1 hour), 291 hours (m.e. 1 hour), and about 291 hours; the mean is 301 hours (m.e. 2 hours). The last two cases were the longest periods observed in June.

This apparent effect on period length probably was produced in two ways: (1) Addition of a parasitic egg or its substitution for a smaller host egg (see Chapter 32) may have caused remaining warbler eggs to receive less heat (compare Hann 1937: 174 with Hofslund 1957; see Eaton 1958: 225, Mayfield 1960: 91–92, pp. 385–386 this study). (2) In all five cases cowbird eggs hatched some 24 hours before warbler eggs; female warblers quickly began to bring food to the young parasites and therefore spent less time warming their own eggs than they otherwise would have. (See p. 248 for the effect of hatching on proportion of time spent on the nest thereafter.)

Effect of clutch size.—Data are too few to permit analysis of the effect of clutch size on length of the incubation period (see Mayfield 1960: 91–92), but the fact that both clutch size and incubation period diminished as the season advanced (Chapter 18) suggests a possible effect. Five of the July incubation periods (Table 78) involved clutches of only three eggs; one produced the shortest incubation period observed. However, the suggestion of an effect draws no support from the two cases in which incubation periods of five-egg clutches are known: 289 hours (m.e. 1.5 hours) and 278 hours (m.e. 10 hours). Neither period is long, especially considering that both began early in the season (9–19 May).

SEQUENCE OF HATCHING

I obtained information on sequence of hatching of two or more eggs in 32 nests. In 27 of these, all eggs whose sequence I knew hatched in the order in which they had been laid. More particularly, for 1 clutch of 4 I knew the hatching sequence of all eggs and for 7 clutches of 4, of 3 eggs; in 16 other cases I knew only that the egg laid last hatched last; finally, for 3 clutches I knew only that egg 1 hatched first.

In the remaining, exceptional instances, sequence of hatching and laying differed, as follows: In 3 nests, egg 4 was the first or second egg to hatch; the last egg to hatch in these same nests was egg 3 in one case and either egg 2 or egg 3 in 2 cases. In another nest, egg 3 hatched first, and in still another egg 2 was one of the last two eggs to hatch.

HOURS AT WHICH EGGS HATCHED

It seems clear that hatching tended to occur during the day. I could fix the hatching time of 70 eggs as falling in the period 0600–2000; 20 additional eggs hatched between 1900 on one day and 0800 on the next. Therefore at least 78% of 90 eggs hatched during a 14-hour period of daylight; 22% hatched during a 13-hour period falling largely at night. In a test of goodness of fit, expected frequencies of hatching during day and night are calculated from the ratio 14:13; adj. Chi-square = 23.1; $df = 1$; $P < 0.001$. Neither my schedule of field work nor the slight overlap between the two time intervals compared can account for this difference. A possible cause may have been that the more frequent activity of the female during daylight stimulated the embryo (compare Weeden 1966: 379). Any slight jar I administered to a hatching egg usually caused the warbler within to respond with an egg-cutting movement of head and neck (see p. 242). Further, females may occasionally have helped hatching young by picking away pieces of shell (see p. 242), an activity that would not be expected during darkness.

Among cases of hatching during daylight were 23 known to have fallen between 0600 and 1300 and 18 known to have fallen between 1300 and 2000. The periods are of equal length, and the hypothesis that hatching occurred randomly during the day cannot be rejected (compare Schrantz 1943: 377, Skutch 1952). Sixteen times of hatching known nearly exactly were randomly distributed between 0635 and 1954.

INTERVAL BETWEEN HATCHING OF FIRST AND FINAL EGGS

The time between the first and last hatching of eggs of the same clutch is the "hatching interval." Data are derived from 39 nests in which all eggs hatched, including 2 nests in which cowbird eggs hatched; cowbird hatching was not considered in determining the hatching interval. The mean hatching interval is rounded to 0.5 hour. When margins of error (calculated and rounded as described on p. 235) for hatching times of the first and last hatchings in each clutch are combined, their total exceeds 12 hours in 15 of the 39 cases; in most analyses that follow, these 15 cases are omitted. In calculating standard deviation, margins of error were ignored.

Hatching intervals for two nests with clutches of 4 eggs are known exactly: 4 hours 45 min and 15 hours 40 min. In 24 cases, including the 2 just referred to, whose margins of error were 12 hours or less, the mean was 13.5 hours (SD 5.4 hours, m.e. 8.5 hours).

Despite complications produced by margins of error and their variability, Table 79 distributes 39 intervals according to length. Summarizing maximum possible lengths, 3 intervals (row 1) were less than 12 hours, 17 additional intervals (rows 2 and 3) less than 24 hours, another 13 intervals (rows 4 and 5) less than 36 hours. Maximum lengths of the remaining cases were too uncertain to justify consideration. The data can also be approached in terms of minimum length, as follows: At least 10 (rows 3 and 5) of 39 intervals exceeded 12 hours; 18 others (rows 4, 5, and 6) may have exceeded 24 hours, and 1 of these

TABLE 79
LENGTH OF HATCHING INTERVAL¹

Hatching interval	N	Mean	m.e. ²
Less than 12 hours	3	5.0	3.0
Possibly less than 12 and certainly less than 24 hours	11	12.5	9.0
More than 12 and less than 24 hours	6	12.5	10.0
Possibly more than 12 hours and possibly more than 24 hours, less than 36 hours	9	18.0	15.0
More than 12 and possibly more than 24 hours, less than 36 hours	4	22.5	6.5
More than 12 and possibly more than 24 hours, possibly 48 hours or more	5	34.5	23.0
More than 24 hours and possibly more than 48 hours	1	46.0	21.0

¹ The hatching interval is measured from first to last hatching of clutches in which all eggs hatched. See page 239 for methods. Two nests in each of which a cowbird egg hatched are included, but the time of that hatching is not considered.

² m.e. = mean margin of error, which is half the time separating 2 inspections between which the first hatching occurred, added to half the time separating 2 inspections between which the last hatching occurred.

(row 7) surely did so; 5 of these same 18 intervals (4 from row 6, row 7) may have exceeded 48 hours.

Variation according to date.—Intervals probably were shorter at early nests, longer at late. Such a difference might be expected: (1) At early nests females incubated less before laying the final egg (p. 200), which would tend toward synchronous development of all eggs. (2) The incubation patch of at least some females was developing during laying of the first clutch (Chapter 20); if time spent incubating before full development of the patch was not maximally effective, differences in hatching times of eggs might be reduced.

Grouping of hatching intervals according to date, using only intervals with margins of error less than 12 hours, is not helpful in testing the foregoing hypothesis because subsamples are too small. However, when dates of very short and very long hatching intervals are considered, short intervals were at early nests and long intervals at later. The two shortest intervals, 4.8 hours and 5.5 hours (m.e. 5.5 hours), were at nests at which incubation started on 9 May and 17 May. The potentially longest intervals and the dates on which incubation began were as follows: 45.5 hours (m.e. 21 hours), 25 June; 44.5 hours (m.e. 26 hours), 26 June; 38.5 hours (m.e. 18.5 hours), 16 July; 30.0 hours (m.e. 17.5 hours), 15 June; 26.0 hours (m.e. 28 hours), 13 June; 24.0 hours (m.e. 24.0 hours), 14 July; and 22.0 hours (m.e. 16 hours), 22 June.

PROCESS OF HATCHING

Position of embryo.—The embryo's position just before hatching (resumed for several hours after hatching) was as follows:

The region of the pygostyle was in the pointed end of the shell, the head in the large end. The neck bent downward full length against the breast and belly, the bill pointing slightly downward and toward the bird's right. The left wing was not folded; its hand extended along the left side of the neck, the distal end almost reaching the head. The left leg and foot were drawn up, with the heel against the belly in the small end of the egg. The right wing was folded, the hand tight along the right side of the neck, the distal end almost touching the base of

the right side of the skull. The right leg and foot were drawn up against the body; the right knee against the left side of the bill, the phalanges against the head over the left eye.

Pipping.—Movement could be felt in unpipped eggs almost ready to hatch; on a smooth flat surface they sometimes rolled slightly. Usually the first indication of imminent hatching was the appearance of one or more short, fine cracks about one-fourth of the way down the egg from its large end. Within 2–7 hours, a convex pointed protuberance (diameter about 1 mm) usually developed, with cracks radiating outward from the point. Some eggs acquired one of these and some two, a few mm apart. Less common were cracked concave areas, i.e. small pit-like dents with many radiating cracks or large dents 5–6 mm across; possibly some were caused by the female's accidentally bumping the eggs together after the shells had become weakened.

The longest interval between formation of the usual convex pip and emergence of the young was at least 21.5 hours. In another case, an egg had not yet hatched 22.5 hours after I found it pipped; a predator then destroyed it. The shortest interval was less than 5 hours (compare Hann 1937: 174, Mayfield 1960: 98).

Emergence of young.—I put a pipped egg on a flat surface and watched it hatch. Timing of events probably was affected by the artificial situation, especially by the absence of much of the touching and jarring the egg probably would have experienced in the nest. In the following description "right" refers to my right as the egg lay before me, small end pointed toward me.

At 0930 the egg showed a slight concave pit about one-fourth the distance from its large end. Shortly before 1500 a protuberance appeared 3 mm to the right of the initial pit. At 1510 the protuberance began to open: a flap of shell (about 1.5 mm in diameter) broke loose on its left side and swung outward like a door hinged on its right side. From this point, successive new breaks, each about 1 mm, gradually converted the original opening into a long, narrow (1.5 mm wide) hole that extended progressively farther toward the right and slightly downward. A ribbon-like strip of shell peeled outward and away from the egg as the hole enlarged; the strip was connected to the rest of the egg on its (moving) right end. Not every cutting movement of the embryo lengthened the ribbon of shell.

The egg tooth was visible at the right edge of the opening; the bird's head was nearly on its side as I faced the egg; the bill pointed to the left along the axis of the developing crack, also slightly downward in the direction of the egg's small end. Movements that resulted in cutting the shell were convulsive and lasted 1 sec or less. Each consisted of an outward and upward extension of the neck and head, forcing the top of the upper mandible against the shell at the point where it was breaking. Accompanying each movement was a slight rotation of the body toward the right. Rotation and the consequent change of the center of gravity was indicated by the fact that after nearly every movement the egg rolled slightly to the left on the flat surface; the advancing edge of the opening was always in the same relative position, facing me. The bill occasionally opened and closed for about 10 sec. About 25 min after the hole had appeared, fluid around the original opening had dried and the shell had changed color over an

area about 10 x 5 mm. At 1550, some 40 min after the opening became apparent, it was 6 mm long; the young had produced this hole by 18 observed head movements at irregular intervals; those that broke the shell were accompanied by a faint popping sound audible about 25 cm away. (A tap on the surface on which the egg rested, or any slight jolt, invariably stimulated a head movement at this stage.) After 1550, movements continued to enlarge the opening, but the egg was now much weakened and began to crack along the line of the cut, both ahead of the cut and backward from the original hole. By 1555, the cut area plus the crack encircled 33% of the egg; each head movement threatened to break off the cap along this line. At 1608, the egg was no longer symmetrical; the embryo had changed position and the cap had been forced upward slightly. At 1612, 66% of the circumference was broken at the cut. At 1623, the bird raised its head and the unbroken segment of the shell snapped; the cap of the egg fell away from the head. The bird immediately moved all limbs 5–10 sec and freed its body from the lower end of the shell; it then lay motionless on its belly, slightly on one side, its body extended and unfolded from the embryonic position.

ADULT BEHAVIOR ASSOCIATED WITH HATCHING

Female behavior.—During the hour or so preceding hatching, females rose to examine and probe the contents of the nest more often than they had earlier in incubation. The behavior of two females that I could see well during the hatching of egg 1 will be described. (1) The female returned to the nest at 1506. At 1525 she rose and pecked into the nest for 30 sec; 1 min later she repeated this for 60 sec, then stood over the eggs. Until 1534 she made brief probes about every 30 sec while looking into the nest. At 1534 she ate half an eggshell. (2) The female returned to the nest at 1024. At 1052 she rose and perched on the rim for 4 min, probing the entire time. She settled briefly, rose and probed, settled again. Between 1052 and 1124, when she left nest, she had perched on the rim and probed or had stood and probed 10 times; total time spent probing was 12.5 min. When she left, I found the nestling lying free between the halves of the shell. This hatching may have taken as little as 4 min or as much as 32 min.

That females sometimes helped young, at least if hatching was prolonged or difficult, was suggested by a case in which an embryo died during hatching. At 1045 the eggshell had been opened and the ribbon-like hole was 3.5 x 1.2 mm; the embryo's upper mandible was in the usual location, but the bird was motionless, probably dead. At 1730, about 20% of the shell had been picked away to form a roughly circular hole around the original opening; much of the embryo's head and body were exposed. It seems safe to assume that the female was responsible.

In all but 2 of about 25 cases, shells of recently hatched eggs, including cowbird eggs, were eaten by the females; this almost always occurred within 1–2 min of hatching. In the exceptional instances, females left the nests for inattentive periods (one of them three different times) without eating the shells; these cases provide evidence that the impulse to dispose of shells by carrying them away was weak in females.

The manner of eating the shell varied. Most commonly, the bird took an entire half by its broken edge, her bill pointing into the concavity. Without attempting to crush the shell into a compact mass and with considerable effortful moving of the head, she then gulped repeatedly; at each gulp a little more of the shell was ingested until finally it was swallowed, in a sense having been eaten whole. The process took 15–90 sec. Occasionally females ate eggshells by picking at or nibbling them or by biting off numerous fragments before swallowing a final large piece.

Male behavior.—In one of the two cases in which females did not eat the shell, a male removed the halves when he left the nest after each of two trips to feed the older nestlings. In the other case I found half the shell on the ground 50 m from the nest and speculate that the male had taken it because the female left three times without it.

EGGS THAT FAILED TO HATCH

Eggs that did not hatch were left in the nest (compare Hann 1937: 175 with Hofslund 1959: 164; see Harding 1931 and Mayfield 1960: 98–99).

CHAPTER 24

TIMING OF CARE OF THE NESTLINGS: BROODING, FEEDING, NEST SANITATION

The nestling interval began on the day the first nestling hatched, also called "hatching day"; subsequent days are "day 2," etc. Daylight is considered to extend from 0430 to 2030 (see p. 205), and the female's active day is measured as described on p. 197. A parent's "feeding day" is the period between its first and last feeding trips to the nest.

Female time budgets cannot be analyzed in terms of attentive and inattentive behavior as in the incubation period, because time spent foraging for nestlings is unknown (see Kendeigh 1952: 49). Attentive activities at the nest can be quantified and are subdivided into (1) brooding the young and (2) perching on the nest rim; subcategories of perching are feeding (manipulating and delivering food, eating feces) and shading (perching motionlessly, whether or not the wings were spread). Waiting for and eating fecal sacs is included under feeding because delivering food and nest sanitation often could not be distinguished when nestlings were small. For similar reasons all motionless perching is classed as shading. Finally, separating cases of feeding from shading sometimes was subjective and allocation of time between these is approximate.

Males engaged in feeding, never in brooding or shading, during my observations; but Walkinshaw saw a male brood for 7 min and also saw him shading (1959; compare Bigglestone 1913, Mousley 1924: 267, Grimes 1936). Activities at the nest were studied both by the nest-inspection method (729 inspections at 181 nests of 116 females) and during 22 day-long nest watches described in the next two paragraphs. Results of neither method are as precise as those for the incubation period, because (1) adult time budgets changed rapidly as young developed, and data for different days of the nestling interval usually cannot be pooled; and (2) nest inspections were less numerous than during incubation, because many nests failed before hatching. Also, inspections did not yield data discriminating precisely among the various attentive behaviors at the nest, a problem that did not arise during incubation.

Most of 22 day-long nest observations (Table 80) were carried out at nests also watched all day during incubation. Numbers applied to females in Chapter 21 are given to them here; males have the same numbers as their mates. One watch was cut short at 1930 when a heavy rain made further observation impossible; data obtained prior to 1915 are used, and certain assumptions are made and stated about attentiveness between 1915 and 2030. At two nests watched on hatching day, the first young hatched no later than 0620; at three others, hatching was no earlier than 1122. These two groups are sometimes discussed separately, as "nests in which hatching was early" and "nests in which hatching was at midday." When brood size is relevant to adult behavior, data from hatching day present a special problem because the number of young changed as time passed. Brood size during the hatching interval (defined on p. 239) is therefore

TABLE 80
ACTIVITIES OF FEMALES DURING DAY-LONG NEST WATCHES, ACCORDING TO DAY OF NESTLING INTERVAL¹

Day of interval	Date	Female ¹	Brood size	Weather			Brooding			Perching at nest				Absent from nest	
				Rain, min falling	Maximum temperature, °C	Exposure to sun, min	Min	%/16 hours	%/24 hours	Feeding	%/16 hours	Shading	%/16 hours	Min	%/16 hours
1	13/6	3	819 min	44	27.8	0	795	83	89	9	1	0	0	156	16
1	14/6	4	555 min	0	27.9	180	743	77	85	35	4	0	0	182	19
1	16/7	5	268 min	140	26.7	0	737	77	85	7	1	0	0	216	23
1	19/7	10	1221 min	0	32.2	30	647	67	78	24	3	13	1	276	29
1	29/5	1	2882 min	0	27.2	80	559	58	72	45	5	0	0	356	37
2	17/7	5	2656 min	0	27.8	0	556	58	72	11	1	8	1	385	40
3	15/6	3	3	0	32.2	60	540	56	71	12	1	164	17	244	25
3	21/7	10	2	0	31.7	0	406	42	62	13	1	210	22	331	35
3	21/7	6	3	22	28.3	0	404	42	61	78	8	0	0	478	50
5	18/6	4	3	138	28.3	180	491	51	67	13	1	153	16	303	32
5	23/7	6	3	165	24.4	0	387	40	60	32	3	0	0	541	56
6	18/6	3	3	120	34.4	90	279*	29	53	14	1	304	32	362*	38
6	21/7	5	3	22	28.3	0	208	22	48	15	2	28	3	709	74
7	25/7	10	2	0	26.7	0	256	27	51	30	3	60	6	613	64
7	25/7	6	3	0	32.2	0	109	11	41	30	3	0	0	821	86
7	22/7	5	3	0	27.8	0	70	7	38	20	2	109	11	761	79
8	21/6	4	3	51	28.9	215	164	17	45	23	2	236	25	537	56
9	21/6	3	2	0	30.0	120	122	13	42	21	2	219	23	598	62
9	24/7	5	3	0	27.2	0	82	9	39	39	4	20	2	819	85
9	27/7	10	2	15	28.9	0	73	8	38	19	2	65	7	803	84
9	27/7	6	3	0	34.4	0	0	0	0	20	2	0	0	940	98
9	6/6	1	3	0	24.4	0	0	0	0	17	2	0	0	943	98

* This watch ended at 1930; the 60 min remaining are arbitrarily assigned 30 min to brooding and 30 min to absence from the nest.

¹ Terms and methods are discussed on pages 244 and 246. Numerical designations of females are those applied to these same individuals in Table 66 and Chapter 21. For feeding of nestlings by these females, see Table 85.

translated into nestling minutes (see Nolan 1958b), which is the sum of numbers of minutes each nestling existed outside the egg between 0430 and 2030.

Results of day-long watches are summarized in Table 80, with rows in order according to day of the nestling interval. Approximate minutes during which rain fell between 0430 and 2030 are shown, omitting occasional almost imperceptible precipitation. All watches were in warm weather; consequently the most important temperature bearing on parental behavior was the maximum, and maximum readings at my observation posts are shown. Minutes of exposure of the nest to the sun between 0830 and 1700 are recorded, with a nest treated as exposed only if the sun shone steadily and without obstruction on the cavity or outside walls. Minutes of brooding are presented as percentages of the 24-hour day on the assumption that females brooded all night; females were on the nest both at darkness and daybreak of the night before and the morning following 20 of the 22 watches. A few terms not defined here will be introduced at more convenient points.

FEMALE'S ACTIVE DAY

Time of first inattentive period.—The earliest time at which a female left a nest containing at least one nestling was 0503, the latest 0544; the mean of 17 cases (17 different individuals) is 0525.3 (SD 12.0 min). I watched five females leave the nest for the first time on at least four days and detected no correlation between times of leaving and of civil twilight, no effect of weather, and no variation according to age of nestlings. However, all multiple watches of individuals were carried on in good weather and, for each female, within a calendar interval perhaps too short to reveal changes associated with changing hour of sunrise.

Walkinshaw (1959) saw a female leave a nest at 0516 EST; young had just hatched.

The mean departure time, 0525, was 22 min earlier than the mean time of departure during incubation; but variances were great (relatively much smaller during the nestling interval), and the means do not differ significantly. Nevertheless, there is evidence that the presence of nestlings caused females to leave earlier than they had before hatching: I selected two samples, one for the incubation period and one for the nestling interval, each consisting of 11 cases supplied by a total of four females; numbers of cases contributed by each individual are the same for both samples. With only one exception, all of each female's departures during incubation were later than all her departures during the nestling interval. In the exceptional instance, a female provided 4 cases for each sample; 3 departure times during incubation were the latest among her total of 8 times, but her remaining incubation-period time was earlier than her latest nestling-interval time. No matter how the 11 pairs of times are matched, provided each matched pair is of data from the same individual, distributions of sign must be 11:0 or 10:1. For 10:1, $P = 0.01$.

Time of end of last inattentive period.—Extreme times at which females returned to the nest for the night were 1952 and 2030. The mean of 24 cases (16 females) is 2012.3 (SD 10.1 min). No factors associated with variation were detected.

TABLE 81
LENGTH OF ACTIVE DAY¹ OF FEMALES DURING NESTLING INTERVAL

Female ²	Date	Day of interval ³	Active day, min
1	29/5*	1	904
3	13/6*	1	840
	15/6	3	873
	21/6	9	919
4	14/6*	1	902
	18/6	5	879
	21/6	8	896
5	16/7*	1	866
	17/7	2	895
	21/7	6	889
	22/7	7	903
	24/7	9	878
6	21/7	3	875
	23/7	5	887
	25/7	7	872
10	19/7	1	865
	21/7	3	888
	24/7	7	872
	27/7	9	887

* Designates days on which hatching began sometime after the female first left the nest.

¹ The active day is measured in minutes from the beginning of the female's first to the end of her last period away from the nest. If the female failed to brood on either night, there is no measurement; see pages 203 and 248.

² Numerical designations are those applied to these same females in Table 66 and Chapter 21.

³ The day the first young hatched, hatching day, is day 1, etc.

The mean, 2012, is 29 min later than the comparable figure for the incubation period (see p. 204); relative variation is less than in data from the incubation period. When the incubation-period and nestling-interval means are compared, $t = 5.33$; $df = 45$; $P < 0.001$. Comparing 10 pairs of matched data from five individuals, with one exception all of each female's times from the incubation period were earlier than all her times from the nestling interval ($P = 0.02$).

Weeden (1966: 374-375, 383) found that Tree Sparrows leave the nest earlier and retire later after eggs hatch than during incubation and that time of retirement changes more than time of departure at dawn.

Length of active day.—Table 81 shows lengths of 19 active days provided by 6 females. Lengths on hatching days when only eggs were present at dawn are marked *; departure times on these days presumably were appropriate to the incubation period. The longest of 15 active days when nestlings were present at dawn was 919 min, the shortest 863 min; the mean is 885.3, or 14 hours 45 min (SD 14.2 min). When a mean is obtained for each female (see p. 213) and an overall mean calculated from these, that figure is also 885 min. The longest of the 4 hatching days when only eggs were present at dawn was 904 min, the shortest 840 min, the mean 878 min.

The mean active day, 885 min, is 56 min longer than the comparable mean during the incubation period (p. 204). With two exceptions all of each individual's active days while incubating were shorter than her active days after hatching. For female 10 (Table 81) incubation-period data were lacking.

Length of interval of night rest.—I saw both a female's retirement at night and her first departure next morning in five cases. Intervals of night rest were 530, 539, 545, 547, and 574 min. The mean is 547 min, or 9 hours 7 min, which

is 36 min less than the mean during incubation (pp. 204–205). However, three data (second through fourth) in the foregoing series of times were produced by one individual.

If the overall mean active-day length, 885 min, calculated from individual means of the 6 females is subtracted from the 24-hour day, the resulting mean interval of night rest is 555 min; extremes among the 6 females were 563 min and 538 min.

FACTORS ASSOCIATED WITH BROODING AND SHADING

Brooding at night.—Age and state of development of the young probably were primary factors determining whether females remained on the nest at night. Examination of nests at and after darkness revealed the presence of females in all cases until the night of day 7, when 1 of 10 females inspected was absent. Thereafter frequencies of absence at night were as follows: on day 8, 1 among 8 cases; on day 9, 5 among 10 cases; on day 10, 6 among 8 cases. Nearly all these nests held three young; thus differences in female behavior probably cannot be attributed to differences in brood size (crowding). Nor did date or weather account for the variation (but I examined no nests during heavy rains at dusk late in the nestling interval).

Two cases, one experimental, provide information on the ability of nestlings to survive the night without being warmed. (1) A female disappeared on day 6 when her nest held four young. The male fed these nestlings that day but almost certainly did not brood them that night; minimum temperature was 18.9°C. He did not brood at night on day 7; minimum temperature was 18.3°C. The young left the nest after a normal nestling interval, and three survived to independence. (2) I put a nestling in its seventh day of life into a nest under construction. The female fed it but did not brood even at night (compare preceding paragraph). Although it had no nestmates to huddle with and 2.5 mm of rain fell during the night (minimum temperature, 16.7°C), the nestling appeared normal next morning.

Brooding and shading during hatching day.—The female was on the nest, either brooding or shading, on about 69% of 104 nest inspections on hatching day (Fig. 23-1), i.e. less often than during fully developed incubation (Chapter 21). In Figure 23-2, based on nest watches, females are separated according to whether eggs hatched early or at midday (see p. 244); percentages of time on the nest were 58% and 67%, respectively. At a nest in which hatching was before or at dawn, Walkinshaw (1959) saw a female brood 63% of 8.6 hours distributed during both morning and afternoon.

Two of the three females whose eggs hatched at midday immediately began to be less attentive at the nest. Female 3 (Table 80), whose first egg hatched at 1122 during an attentive period, brooded 90% of the time before that period and 74% after it. Female 5 brooded 78% of the time before the attentive period in which hatching began (at 1525) and 57% thereafter. However, female 4 brooded more (72%) after the first egg hatched (at 1432) than before (66%).

Brooding and shading during days 2 through 9.—Daily percentages (compare Walkinshaw 1959) shown in Figure 23-1 and 23-2 need no comment, except with

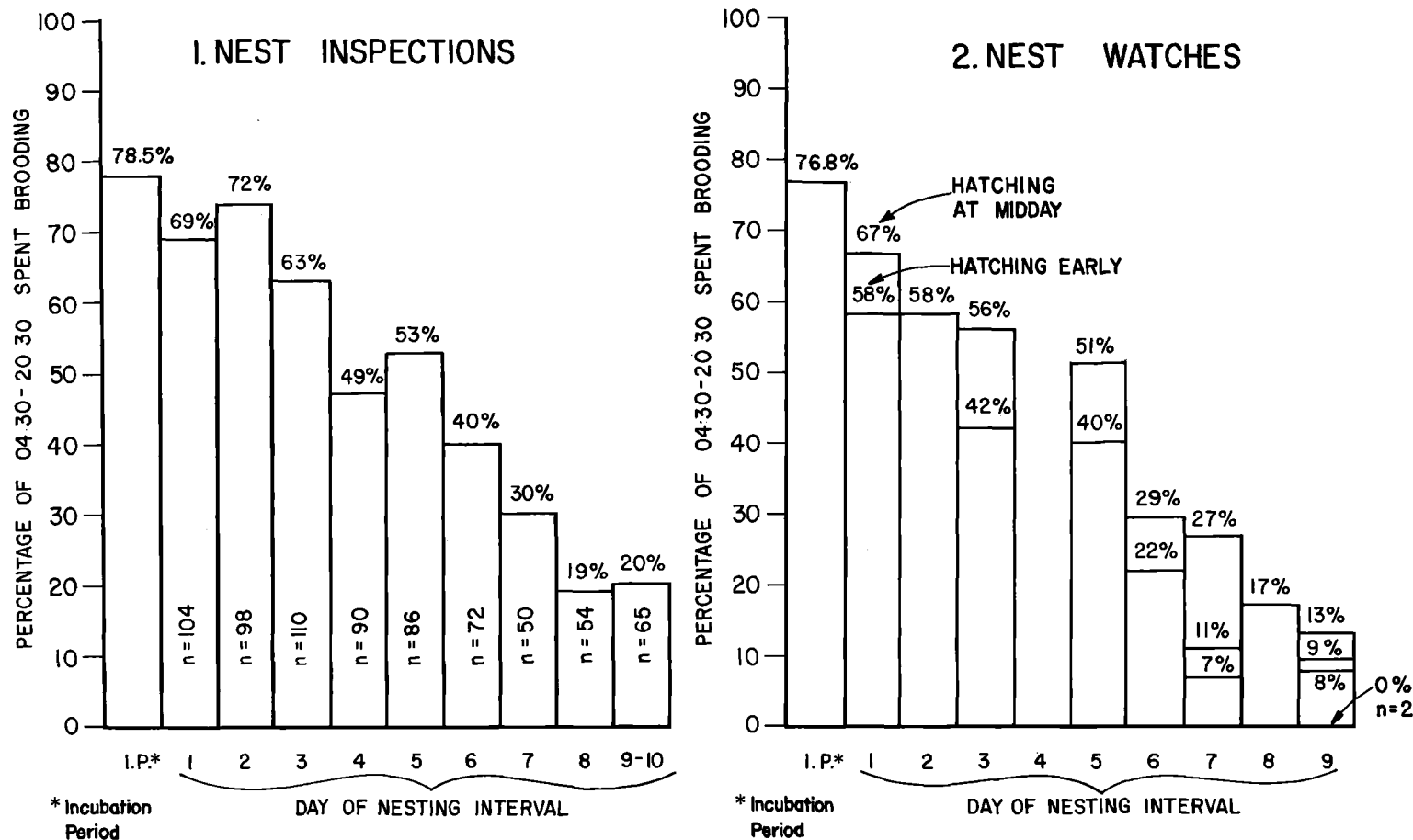


FIGURE 23. Percentage of day (0430-2030) spent on the nest by females, according to day of the nestling interval, compared with percentage of attentiveness during the incubation period. The left-hand graph is based on 729 nest inspections, with the number of inspections per day shown in the columns. The right-hand graph is based on day-long nest watches; each percentage represents 1 watch, except that on day 1 data for 2 watches and for 3 watches were pooled and the respective percentages based on the pooled data. See text and Table 80.

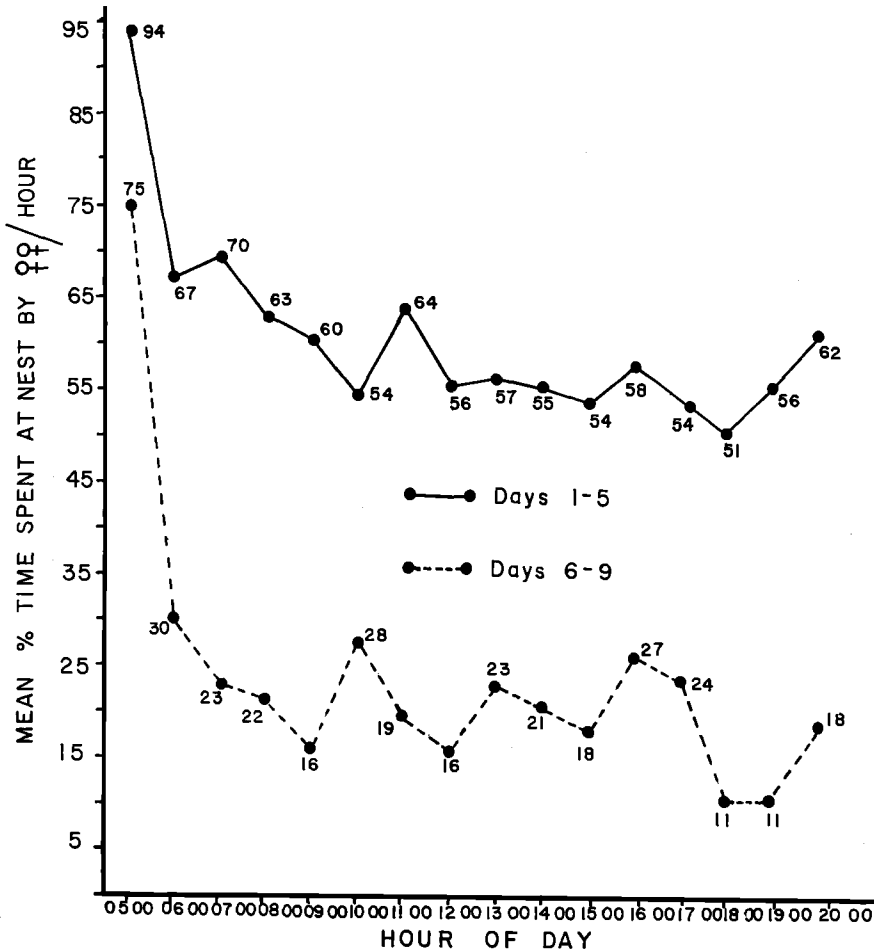


FIGURE 24. Percentage of time spent by females at the nest during day-long watches in the nestling interval, according to hour of day. The upper curve is based on eight watches from days 1-5 of the interval; watches on hatching day at nests in which hatching was at midday are excluded. The lower curve is based on 11 watches from days 6-9 of the interval. Time is eastern standard. Hours run from 30 min before to 30 min after times designated, e.g. from 0630-0730.

respect to differences obtained by nest-inspection and nest-watch methods. Inspections did not permit discrimination between brooding and shading, and Figure 23-1 therefore includes both, whereas Figure 23-2 shows only brooding. This accounts for the consistently higher percentages shown in Figure 23-1. Considering that shading was less common during the first 5 days of the nestling interval than it was from the day 6 onward (Table 80), the similarity in the two graphs in Figure 23 is interesting. It suggests either that motivations for shading and brooding were the same or similar or that, if different, they varied approximately in synchrony.

Brooding and shading during the day, according to hour.—Figure 24 indicates hourly (see p. 207) percentages of brooding and shading during day-long watches.

One of the two curves is based on 8 watches from hatching day through day 5 (excluding 3 watches when hatching began at midday); the other, for the later part of the nestling interval, is based on 11 watches from days 6 through 9.

Resemblance between the shape of the curve for the first five days of the interval and that of the curve of attentiveness during the incubation period (Fig. 18) is striking. Apparent in both are the sharp decline between dawn and mid-morning, temporary reversal of this trend in late morning followed by a further decline to a low point in late afternoon, and a rise before dark. In the curve for the second half of the nestling interval many characteristics of the incubation-period curve are still discernable. If "[b]rooding of young is merely a continuation of incubation behavior . . ." (Davis 1955: 290; compare Emlen 1941; Lehrman 1961: 1302–1304; see pp. 231–233), these similarities are not surprising.

Brooding and shading during day, according to weather and nest exposure.—Nest inspections during cool weather were too few to reveal effects of low air temperature. Exposure to the sun, especially on hot days, evidently caused females to increase time at the nest, as suggested by Table 80. Inspection of the table reveals five watches during which females were absent from the nest less than would have been expected: 25% on day 3, 32% on day 5, 38% on day 6, 56% on day 8, and 62% on day 9. Columns 6 and 7 show that these were the only watches, except for irrelevant cases on hatching day, during which nests were exposed to the sun and that all five occurred on hot days. Rainfall (see below) probably contributed to the high attentiveness in three of the five cases, but it seems safe to conclude that exposure had an important effect in all.

Increased attentiveness at exposed nests on hot days led to more brooding as well as more shading (Table 80). For example, on day 9 female 3 brooded 13% of the time and shaded 23%; both percentages are much higher than those of other females whose nests were watched throughout day 9.

Table 80 also suggests that females spent more time at the nest when showers were frequent, but, as noted above, these cases are ambiguous because the days were hot and the nests exposed. Evidence of rain's effect on one female is the following: I watched a nest between 0800 and 1200 on day 8 (rainless), day 9 (hard rain half the time), and day 10 (rainless). In chronological order, the female brooded 10%, 41%, 7% of these watches (compare Nice 1930b). At least 10 times when it began to rain during day-long watches females returned to nests without bringing food and left, sometimes after unusually long periods of brooding (compare Mousley 1924: 281), as soon as rain stopped. These were among the few cases in which females returned to nests without food (see below, Table 85).

Effects of size of brood and male participation in feeding on brooding and shading during the day.—It might be expected that the more nestlings a female had to feed, the less time she would spend at the nest, but brood size varied too little (Table 80) to permit that factor to be investigated with available information. However, a related point, in that it involves the female's problem of allocating time between sheltering and feeding nestlings, can be considered. That problem is the effect of male assistance on the female's behavior. It seems clear that females with sole responsibility for providing food usually spent more time away from

TABLE 82
PERIODS OF INDIVIDUAL FEMALES AT AND AWAY FROM NEST DURING
DAY-LONG NEST WATCHES IN NESTLING INTERVAL

Female ¹	Day of interval ²	Periods at nest ³				Periods away from nest ³			
		N	Length, min			N	Length, min		
			Mean	Extremes	Median		Mean	Extremes	Median
1	1*	39	14	2-43	10	41	9	1-24	9
	9	0	—	—	—	142	6	1-28	5
3	1*	32	21	4-109	14	36	4	1-14	4
	3	25	25	2-62	20	27	9	1-24	9
	6 ⁴	25	20	12-53	17	30	11	1-27	12
	9	21	15	2-84	10	52	12	1-67	9
4	1*	25	26	2-151	26	26	7	1-21	5
	5	22	27	4-56	21	23	13	1-60	8
	8	29	16	1-50	11	51	11	2-54	8
	1*	18	36	2-102	27	19	11	2-26	10
5	2	32	16	3-54	11	36	11	1-36	8
	6	15	12	2-42	11	31	23	3-65	20
	7	10	14	3-30	14	35	22	1-59	20
	9	4	6	2-18	10	45	19	2-83	13
6	3	47	8	1-19	7	62	8	1-28	7
	5	33	10	1-43	9	69	8	1-21	7
	7	4	5	4-7	5	89	10	1-30	9
	9	0	—	—	—	98	9	1-42	6
10	1*	31	19	3-64	14	34	8	2-22	7
	3	29	19	3-49	16	32	10	1-28	8
	7	27	9	1-25	9	43	14	3-46	13
	9	5	5	3-7	5	95	9	1-39	8

* The first young hatched at the following times during watches on day 1: female 1, 0620; female 3, 1122; female 4, 1432; female 5, 1525; female 10, before daylight.

¹ Numerical designations are those applied to the same females in Table 66 and Chapter 21.

² The day the first young hatched, hatching day, is day 1, etc.

³ Methods used in counting periods and measuring period lengths are described on pages 252-253.

⁴ This watch ended prematurely at 1930, 30-60 min before the end of the female's active day.

the nest and less time brooding and shading than did mated females (see also data on feeding trips by unassisted females, p. 263).

Female 6 had no mate during any day-long watch, and female 10 had none on day 9. The following compares time away from the nest by these two with time away by females whose mates helped care for young. In cases marked *, females did not brood at night and percentages are based on length of feeding day instead of total day length: Day 3—female 6, 50%; two females with mates, 25% and 35%. Day 5—female 6, 56%; female with mate, 32%. Day 7—female 6, 86%; two females with mates, 64% and 79%. Day 9—female 6, 98%*; female 10, 84%; three females with mates, 62, 85, 93%* (possibly significantly, female 10 had only two nestlings whereas the mated females, i.e. pairs, each had three).

Age of female as related to brooding and shading during the day.—No nest of a yearling was watched all day. Nest inspections suggested no age-associated differences in attentiveness.

FEMALE'S PERIODS AT AND AWAY FROM NEST

This section, based on the day-long watches, distinguishes between occasions when females left the nest immediately (a few seconds) after feeding and disposing of feces and those when they remained and brooded or shaded. The

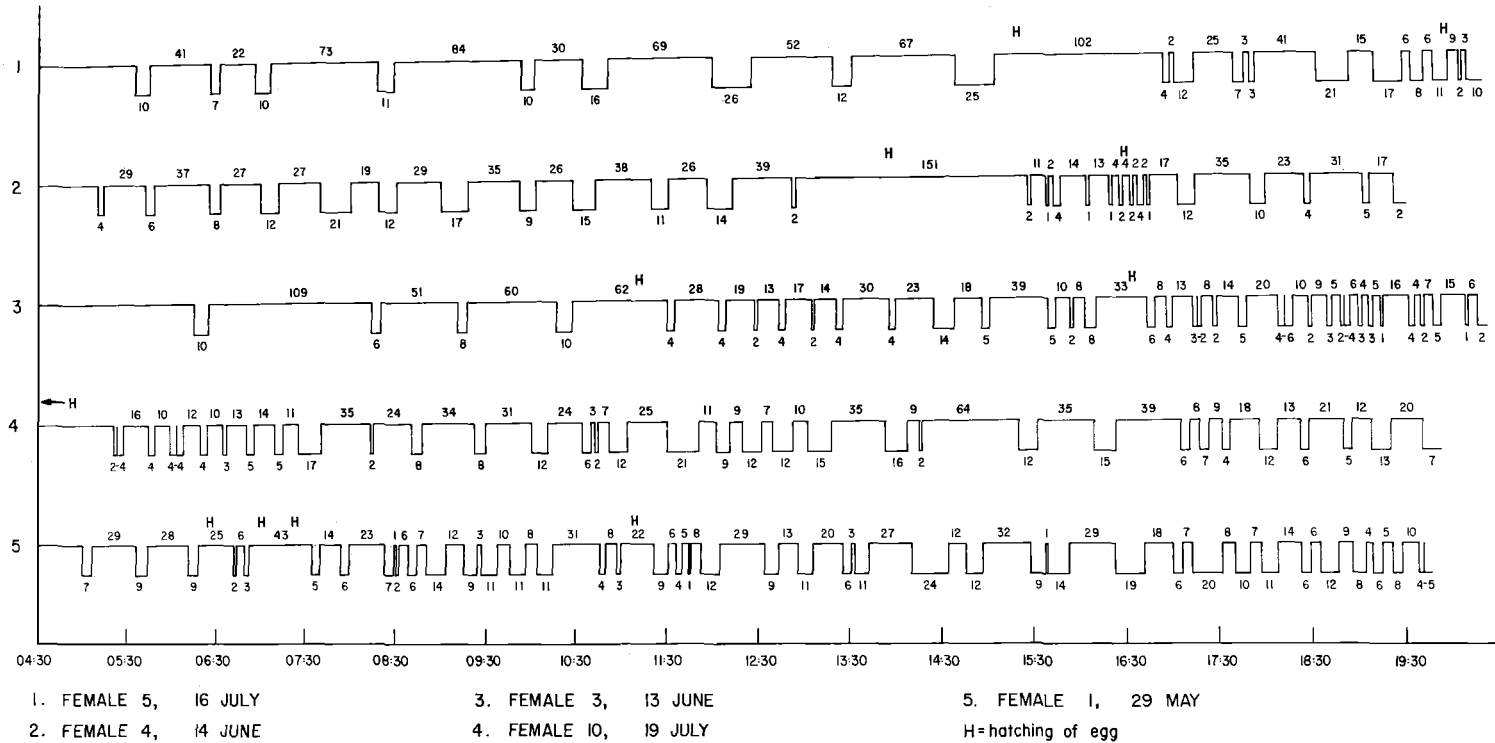


FIGURE 25. Attentive-inattentive rhythms of females at nests watched throughout hatching day. Time (eastern standard) is shown at the bottom. Hours run from 30 min before to 30 min after times designated, e.g. from 0630–0730. Each jagged line represents 1 day; upper segments indicate attentive periods, lower segments inattentive periods; numbers show lengths of periods in minutes. H indicates the hatching of an egg at the time indicated. Designations of females and dates refer to Table 80.

TABLE 83
PERIODS OF FEMALES AT AND AWAY FROM NEST DURING DAY-LONG
WATCHES, ACCORDING TO DAY OF NESTLING INTERVAL¹

	Day									
	1, hatch at midday ³	1, hatch early ³	2	3	4	5	6 ⁴	7	8	9
Day-long watches (N)	3	2	1	3	0	2	2	3	1	5
Periods at nest ²										
Mean periods per watch (N)	25	35	32	34	—	27	20	14	29	6
Length, min										
Mean	25.3	16.2	15.9	15.3	—	16.5	17.2	10.1	12.0	11.5
Extremes	13-2	47-1	43-2	51-1	—	66-1	53-2	30-1	54-2	84-2
SD	27.4	11.9	13.5	13.4	—	14.4	12.6	6.7	11.8	22.1
Median	17	12	11	10	—	11	15	9	7	8
Periods away from nest ²										
Mean periods per watch (N)	27	38	36	40	—	46	31	56	51	86
Length, min										
Mean	6.9	8.5	10.7	8.5	—	9.4	17.2	13.4	10.8	9.4
Extremes	26-1	24-1	36-1	28-1	—	60-1	65-1	64-1	52-1	83-1
SD	5.6	5.1	8.9	6.5	—	8.4	13.1	11.2	10.3	9.9
Median	5	8	8	8	—	7	16	11	8	6
Number of periods at nest as % of number of periods away	93	92	89	85	—	59	65	25	57	7

¹ The day the first young hatched, hatching day, is day 1, etc.

² Methods used in counting periods and measuring lengths are described on pages 252-253.

³ The first young hatched at 1122, 1433, and 1525, respectively, in the nests in which hatching was at mid-day. In the nests where hatching was early, the first young hatched before daylight in one and at 0620 in the other.

⁴ One watch was terminated prematurely, at 1930; there were probably a few additional periods before the day's end.

latter, excluding the interval of night rest, are "periods at the nest," and absences are "periods away from the nest." Lengths of all periods are rounded to the nearest minute, except that a few absences lasted less than 30 sec but are counted as 1 min. Lengths and numbers of periods at and away during each day-long observation are summarized in Table 82.

Hatching day.—Changes in both length and number of periods began immediately after the first young hatched, as shown in Figure 25 and Table 83. (1) Some females (Fig. 25-1 and 25-2) remained on the nest for extremely long periods, 102 and 151 min, during the initial hatching. (2) Lengths of periods at and away then decreased immediately (compare Walkinshaw 1959, Weeden 1966). For example, the median period at nests in which hatching was early was 12 min; the median period away was 8 min (Table 83); compare the much longer median attentive and inattentive periods late in incubation (Table 66). Decrease in length of periods at the nest was considerably greater than decrease in length of periods away. (3) As periods were abbreviated, their number increased. For example, female 1 had an aggregate 47 attentive and inattentive periods the day before hatching (28 May, Table 66), 80 periods at and away on hatching day; compare also numbers of female periods at nests in which hatching was early and at midday (Table 83). Contributing to the increased time away from the nest was the fact that females sometimes took more than one period away in

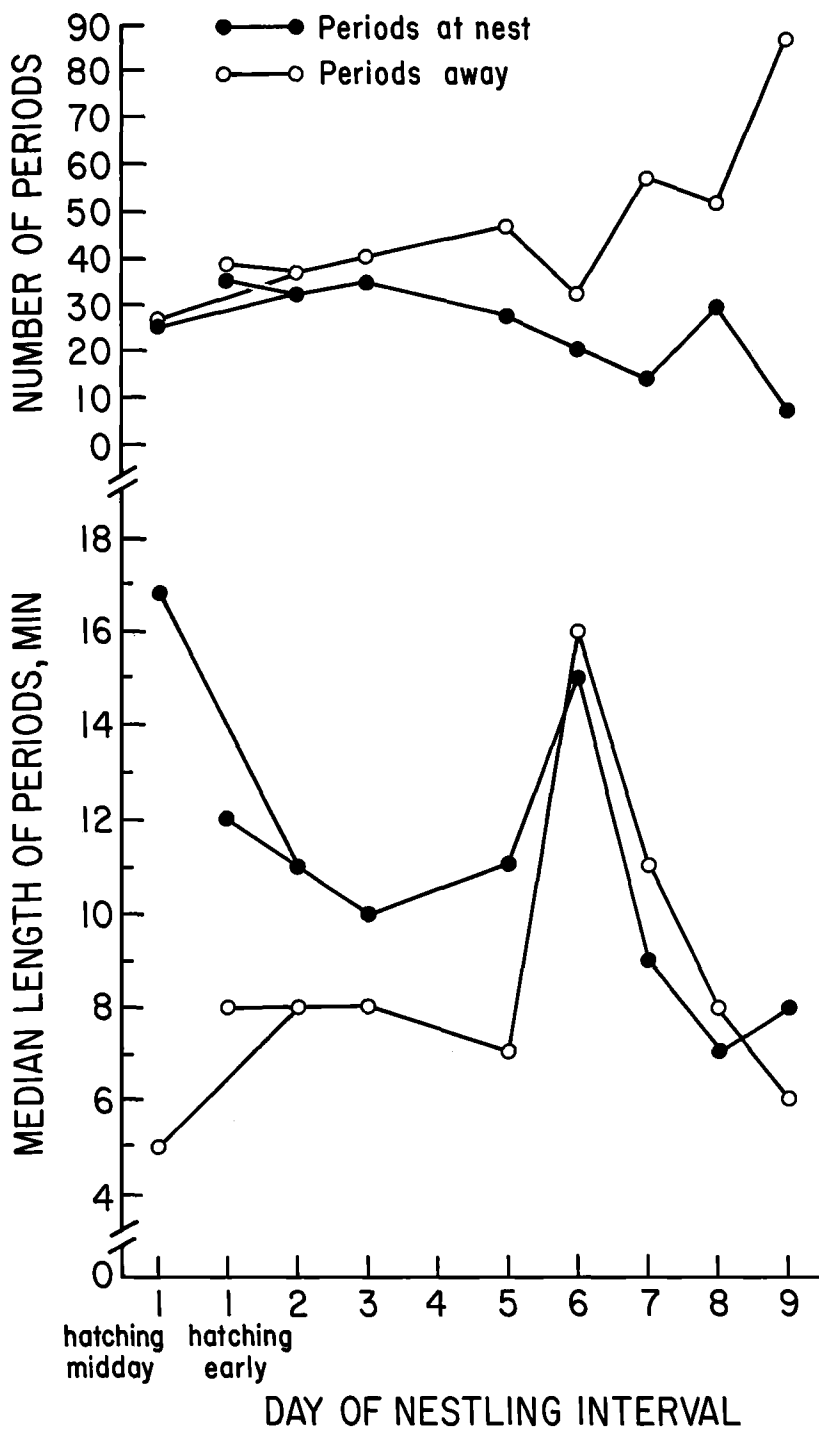


FIGURE 26. Number and median length of female periods at and away from the nest, according to day of the nestling interval. Data were obtained during day-long nest watches; see text and Table 82.

TABLE 84

LENGTH OF FEMALES' PERIODS¹ AT AND AWAY FROM NEST DURING 19² DAY-LONG NEST WATCHES, ACCORDING TO HOUR OF DAY OF NESTLING INTERVAL

Hour ³	Periods at nest (Length, min)					Periods away from nest (Length, min)					N periods at nest as % of N periods away
	N ³	Mean	Extremes	SD	Median	N ³	Mean	Extremes	SD	Median	
0500	10	16.1	43-3	15.1	10	25	5.7	27-1	5.3	3	40
0600	37	13.8	51-2	10.9	11	108	6.1	32-1	5.4	4	34
0700	36	13.3	43-2	8.6	11.5	83	7.1	30-1	5.6	5	43
0800	27	16.0	54-1	14.4	9	76	10.0	60-1	8.8	6	36
0900	26	15.5	46-2	13.7	9.5	72	12.2	83-1	11.9	9	36
1000	26	16.8	42-5	8.7	11.5	58	11.4	52-2	9.2	9	45
1100	26	17.3	66-1	17.9	11.5	58	11.9	41-1	9.6	8	45
1200	26	12.2	50-2	11.0	8	63	13.0	65-1	12.4	9	41
1300	27	15.6	61-3	11.6	13	65	9.8	43-1	7.9	9	42
1400	21	17.0	53-2	13.5	10	62	13.4	59-1	10.5	10	34
1500	24	17.2	64-1	15.1	13.5	59	13.2	64-1	11.9	11	41
1600	23	17.6	84-1	20.6	14	51	11.6	38-3	6.5	12	45
1700	24	12.5	39-3	8.0	11	59	12.6	33-1	8.2	10	41
1800	29	11.0	59-2	6.9	10	68	12.4	59-1	11.1	9	43
1900 ⁴	24	10.1	36-3	7.3	8.5	68	11.5	67-1	12.1	8	35
2000 ⁴	12	8.4	20-4	4.9	7	60	6.5	41-1	5.7	5.5	20

¹ Methods used in counting periods and measuring lengths are described on pages 252-253.

² See Table 80 for details concerning the watches; omitted are the 3 watches at nests in which hatching was at midday.

³ Periods are assigned to the hour in which they began. Hours began 30 min before and ended 30 min after the times used to designate them; e.g. 0700 is the period 0630-0730. Females never left the nest as early as 0430 and rarely remained away until 2030; the 2 terminal hours are therefore fractional.

⁴ One watch was ended prematurely at 1930; the female probably would have gone to and from the nest a few more times before dark.

succession, bringing food and leaving immediately (Fig. 25-3, at about 1730; Fig. 25-5, 1930-2030). As a result, the number of periods at the nest was only 93% of the number of periods away.

Days 2-9.—Figure 26 graphs daily changes in median length and in number of periods, using pooled data from Table 83. (1) Number of periods at the nest changed little until day 4 (for which there was no information) or day 5 and then decreased, probably steadily. (On the only day-8 watch the number was large, very likely because of rain and the exposure to the sun.) (2) Number of periods away increased gradually during the first half of the nestling interval, then on about day 7 rose sharply. (Again, exceptions to this trend on days 6 and 8 are probably attributable to exposure and rain on two of the three nests watched on those days.) (3) Number of periods at the nest fell from 93% of periods away on hatching day to 7% on day 9. (4) Lengths of periods per day varied irregularly. By day 9 periods at the nest had become much shorter while periods away were about the same as on hatching day. From day 6 onward, periods away from the nest tended to be longer than periods at it. (5) A temporary increase in lengths of both kinds of periods in the middle of the nestling interval is unexplained.

Variation according to hour of day.—Table 84 and Figure 27 summarize numbers and lengths of periods according to the hour (see p. 207) in which they began. Data are taken from all day-long nest watches except the three during which hatching was at midday, and they are pooled without regard to advance of the nestling interval; analysis (not shown) reveals that this pooling does not produce

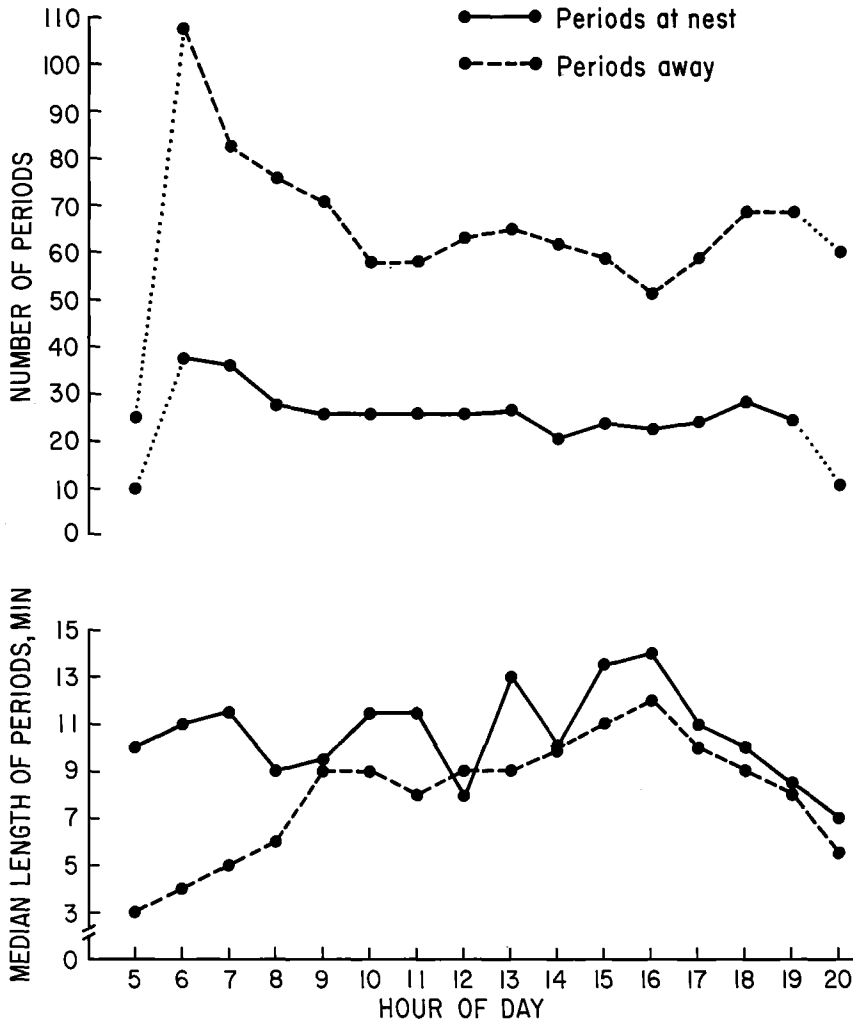


FIGURE 27. Number and median length of female periods at and away from the nest during the nestling interval, according to hour of day. Time is eastern standard. Hours run from 30 min before to 30 min after times designated, e.g. from 0630–0730. Periods are assigned to the hours in which they began. Data were obtained during 19 day-long nest watches, excluding 3 watches at nests in which hatching was at midday; see text and Table 84. Dotted lines in the upper figure indicate hours in which the females' active day (pages 197, 247) started or ended; thus these hours were fractional, which reduced numbers of periods during them.

misleading results. Similarly, use of unequal numbers of watches per female does not affect results importantly and is accepted to increase sample size.

Lengths of periods: As for periods at the nest, most hourly fluctuation in median length appears unpatterned, suggesting no important variation of that kind. Longest periods at the nest were in the afternoons, probably because several watches were at nests exposed to the sun at that time and shaded by females. The steady decrease in length of periods at the nest from 1600 to 2000 (compare Cox's 1960 similar observations on the Mourning Warbler) is doubtless partly

attributable to change in position of the sun; also, number of feedings increased at this time (see below).

The median period away was shortest at dawn, increased steadily until 0900, then remained about the same through 1300. At 1400 another gradual increase began; the longest median of the day was at 1600, followed by a steady decline in length until nightfall. This variation (Fig. 27) closely resembles hourly changes in median length of inattentive periods during incubation (Fig. 21).

Despite the increased length of periods at the nest at 1600, this was probably the time of maximum inattentiveness during the nestling interval. Note that periods at the nest were only about half as numerous as periods away (see Table 84). Feeding trips of both parents were fewer at 1600 than at any other hour (see below).

Numbers of periods: No female whose periods are analyzed in Table 84 or Figure 27 began the active day as early as 0430, and only one ended it as late as 2030 (see Table 80). Therefore, the intervals 0500 and 2000 are fractional for present purposes and are not to be compared with other intervals.

Probably only two significant changes in numbers of periods at the nest occurred during the day: (1) Periods per hour were most numerous prior to 0800, after which the pace of feeding slackened considerably (p. 265). (2) Periods were least numerous from 1400 through 1700, possibly through 1900.

Periods away were most frequent just after dawn (when feeding was rapid), both absolutely and relative to number of periods at the nest; at 0600 females left the nest immediately after 66% of all feeding trips. From 0600 to 1000 frequency of periods away declined sharply, then increased slightly until 1300. A decline beginning at 1400 reached the day's low point at 1600. From 1700 to the end of the day, feeding trips became more frequent and periods away grew shorter; frequency of these periods, both absolute and relative to periods at the nest, increased.

Variation according to weather.—Exposure to sun caused females to prolong periods at the nest and to abbreviate periods away during the heat of the day (see p. 213); examples are given on pages 263–264 in connection with rates of feeding the young (compare Bigglestone 1913 and Harrison 1951). Hard rains also appeared to prolong periods at the nest and caused some females to return immediately when away from it; see page 251.

FEEDING TRIPS: TIMING AND FREQUENCY

First feeding after hatching: females.—Females differed as to promptness of feeding after the first young hatched. In 5 observed cases, 1 female brought food at the end of the first period away after hatching (about 21 min after the young hatched); 2 did so at the end of the second period away (about 87 and 127 min after hatching); 1 may have brought food at the end of her second period away (40 min after hatching) and certainly did so at the end of her third (61 min). The fifth female had not brought food by the end of her fourth period away, 124 min after hatching.

Once, the first young had hatched during the night before observation began; the female first left the nest at 0539 and returned with food at 0541 (compare Walkinshaw 1959). See also the experiments on pages 231–232.

First feeding after hatching: males.—At the 5 nests watched throughout hatching day, 3 males fed 183, 325, and 598 min, respectively, after the first young hatched (see Walkinshaw 1959). Two did not feed that day in the 548 min and 305 min between first hatching and 2030 (i.e. darkness). One of these two brought food first at 0758 next morning; the other had not yet fed when I quit observing at 1010 on day 2; he was feeding on the morning of day 3.

In 20 experiments (see pp. 233–234) I placed young in nests under incubation, almost invariably doing so at or before 0800. At least 11 and probably more males fed on the day of introduction, 2 of them 17 and 30 min, respectively, after accompanying mates to the nest at the end of the inattentive period during which I had introduced the young.

One male was unusually neglectful of a brood: During 12 hours' observation, approximately equally distributed between morning and afternoon on days 1–5 and 8–9 of the nestling interval, he did not feed. On day 6 he fed as often as the female, but on day 7 he brought food only twice compared to her 14 times.

Times of first and last feedings of day: females.—The day's first feeding by the female took place when she returned from her initial period away, with one exception among 18 day-long watches at nests that held nestlings at the beginning of the day; the exceptional female fed after her second period away. The earliest first feeding was at 0508, the latest at 0605 (see Table 85); the mean of 18 cases was 0532.9 (SD 14.1 min).

The last feeding trip always coincided with the female's return to the nest for the night, the times of which are summarized on pages 246–247. Interestingly, when females spent both the night before and the night after my nest watch off the nest (footnote 8 in Table 85), the first and last food was brought at about the same times as on all other nest watches.

The longest feeding day lasted 908 min, the shortest 835 min; the mean of 17 cases was 874 (SD 19.0 min). For further analysis see the discussion of the female's active day, page 247.

Times of first and last feeding of day: males.—Counting only males known to have discovered the existence of their nestlings before the day in question, extreme times of the first feeding of the day were 0503 and 0625 (see Table 85); the mean of 11 cases was 0540.1 (SD 24.2 min). On these same mornings the mean time of first feeding by the males' mates was 21 min earlier than the males' mean; two males fed earlier than their mates.

The morning on which a female fed earliest (0508) was also the morning on which a male fed earliest (0503); and when a female fed at the latest time (0557), her mate's time was the second latest for any male (0609). In the 11 cases in which times were known for both members of a pair, $r_s = 0.77$; P (one-tailed) < 0.01 . Considering the great range between earliest and latest first feeding times, the correlation of pairs' times probably does not reflect independent but similar responses to some environmental stimulus. More likely, behavior of one member of the pair was affected by behavior of the other.

Latest male feedings ranged between 1811 and 2021; the mean of 14 cases was 1937.4 (SD 38.1 min). The mean time for the mates of these males on the same evenings was 34 min later; one male fed later than his mate (by 29 min). Times of feedings by members of the pair did not correlate.

TABLE 85
TRIPS TO NEST WITH FOOD AND YOUNG FED DURING 22 DAY-LONG WATCHES, ACCORDING TO SEX OF PARENT AND DAY OF
NESTLING INTERVAL

Day ¹	Pair ²	Brood size ³	Female			Male			Total, males and females		Meals/nestling	
			Time of first feeding	Time of last feeding	Feeding trips/day ⁴	Time of first feeding	Time of last feeding	Feeding trips/day ⁴	N	% by male	N ⁵	Rate, min ⁶
1	3	819 min	1130	2010	30 (1)	no feeding		0	30	0	20	29
1	4	555 min	1640	2012	14 (4)	1736	2010	9	23	39	16	23
1	5	268 min	1652	2013	8 (2)	no feeding		0	8	0	8	38
1	10	1221 min	0541	2004	33 (1)	1508	2004	13 (1)	46	28	37	24
1	1	2882 min	0651	1957	37 (1)	1159	1949	30	67	45	18	43
2	5	2656 min	0527	2015	35	0758	1811	10	45	22	18	50
3	3	3	0520	1952	26 (1)	0530	2021	33	59	56	21	43
3	10	2	0526	2013	32	0529	1956	21	53	40	26	35
3	6	3	0543	2005	62	no male		—	62	0	23	39
5	4	3	0532	2003	19 (3)	0526	1825	51	70	73	25	36
5	6	3	0605	2000	69	no male		—	69	0	25	36
6	3 ⁷	3	0508	1901 ⁷	29 (1)	0503	1759 ⁷	38	67	57	24	38
6	5	3	0542	2022	31	0625	1932	26	57	46	21	43
7	10	2	0538	2005	44	0602	1935	24	68	35	37	24
7	6	3	0541	2007	89	no male		—	89	0	32	28
7	5	3	0527	2030	36	0547	1950	39	75	52	27	33
8	4	3	0519	2004	47 (3)	0531	2000	67	114	59	41	22
9	3	2	0519	2027	52	0516	1919	41	93	44	51	18
9	5	3	0557	2008	45	0609	1925	38	83	46	30	30
9	10	2	0531	2016	96 (1)	no male		—	96	0	52	17
9 ⁸	6	3	0538	2001	98	no male		—	98	0	36	25
9 ⁸	1	3	0520	2019	142	0544	2004	76	218	35	79	11

¹ The first day of the nestling interval, hatching day, is the day on which the first young hatched.

² Numerical designations are those applied to these same females in Table 66 and Chapter 21.

³ Brood size is stated in nestling minutes whenever any egg hatched after the female left the nest for the first time on day 1. See methods on pages 244, 246.

⁴ Numbers not in parentheses indicate trips on which food was brought; numbers in parentheses indicate trips (after hatching) without food.

⁵ Number of young fed per trip is calculated as 1.1 except on day 1, when the number is 1.0; see page 270.

⁶ Rate in minutes is calculated for a 900-min day; see page 270. On watches during which one or more eggs hatched, only number of meals of the first young that hatched is shown, calculated as described on page 270. In one case in which a nestling hatched on day 2, the table shows only the calculated number of meals of nestmates that had hatched on day 1, calculated as described on page 270.

⁷ This watch ended prematurely at 1930; see pages 244 and 265.

⁸ Females spent both the preceding and the subsequent nights off the nest. Before and after all other days the females spent the night on the nest.

The shortest feeding day of males (excluding days of the hatching interval) lasted 779 min, the longest 891 min; the mean of 10 cases was 834.8 min (SD 38.7 min).

Daily mean number of feeding trips for nestling interval.—Some writers present mean rates of feeding without differentiating among days of the nestling interval or among brood sizes. Therefore, for comparative purposes I have calculated the mean number of feeding trips on 22 day-long watches, proceeding as follows: I obtained a daily mean for each day of the nestling interval beginning with hatching day (excluding nests at which hatching was at midday), then obtained an overall mean from the daily means. The daily mean for day 4 was obtained by linear interpolation from day-3 and day-5 means.

The overall mean for the first 9 days of nest life is 74 feeding trips per day. However, many broods remained in the nest through day 10 or 11. Since feeding rate evidently continued to increase until nest leaving (see below), the overall mean for such long nestling intervals might reach 80.

Share of total feeding trips by each sex; male's time budget.—Relative contributions to feeding by the members of the pair probably did not change as the nestling interval advanced (see below). I have therefore calculated the percentage that each sex contributed to the total feeding trips, pooling all day-long watches except watches at nests of females without mates and nests in which hatching was at midday. Of 1115 feeding trips, the female made 608, or 54.5%; adj. Chi-square = 9.0; df = 1; $P < 0.005$. Beyond this difference, nests tended by females without male assistance were much more frequent than nests tended by unassisted males (see Table 85); I observed only one instance in which a male fed nestlings after losing a mate. Therefore from the perspective of feeding trips to all nestlings produced by the population, females performed considerably more work. See also the discussion of quantities of food per trip, page 270.

Walkinshaw (1959) watched a nest of Prairie Warblers for about 26 hours; the male fed 51 times, the female 61 (54%).

The female's allocation of time during the nestling interval is reflected in various tables in this chapter, especially Table 80. This paragraph estimates the proportion of the average day (0430–2030) devoted by an assisting male to foraging for and delivering food to nestlings of advanced age. If he made about 40 feeding trips (see Table 85), spent some 15 sec at the nest on each trip (see Table 87, below), and sang 1 min near the nest before going to it and 30 sec near it after leaving (Chapter 25), a total of 1.2 hours would be consumed by activities associated with delivering food. The time required to find this food is unknown; for a suggestion we can look to the minimum interval between feeding trips of individuals that seemed to be bringing items to the nest as rapidly as possible: Occasional females fed at a rate of once every 3 min (see p. 263). Assuming that males required an average 3 min to find the items brought on a single trip, at least 2 hours would be required to find the food delivered on 40 trips. It appears, then, that late in the nestling interval a male might spend some 3.2 hours (about 20% of daylight) feeding his young.

Variation in number of feeding trips, according to day of nestling interval.—Adults made more feeding trips per day as nestlings grew older (compare Nice 1943: 231–233). To analyze this increase I have selected three nests, each

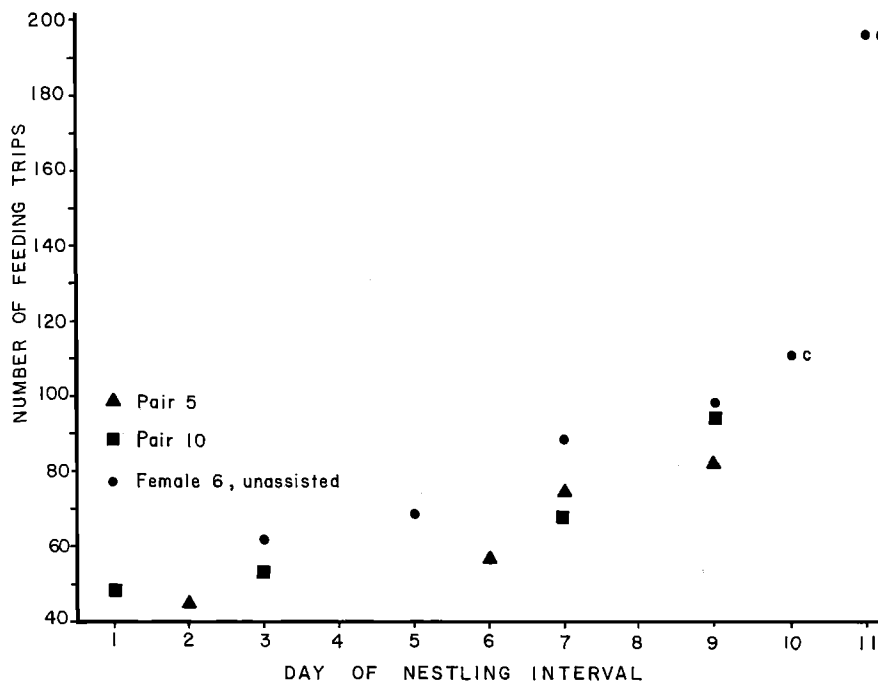


FIGURE 28. Total male and female feeding trips to three nests, according to day of nestling interval. Counts were made during day-long watches, except that totals for female 6 on days 10 and 11 (marked C) were calculated by extrapolation from 6-hour watches. Designations of birds follows Table 80, which gives details, e.g. brood size.

watched all day on 4 days (nests of pair 5, female 6, and pair 10 in Table 85; male 10 disappeared between watches on days 7 and 9). Numbers of nestlings in these nests remained unchanged throughout the interval. To the four observed totals for female 6 were added two calculated totals, derived as follows: I watched female 6's nest throughout day 9 and during the first 6 hours of both days 10 and 11. On the assumption that the hourly distribution of all trips on day 9 was about the same as the distributions on days 10 and 11, I extrapolated from observed data for parts of days 10 and 11 to hypothetical totals for the full days. The resulting six totals for female 6 may be especially useful for detecting daily variations in frequency of feeding trips; male-female interactions cannot have affected the data, the weather was uniformly fair, and female 6's nest was never exposed to the sun.

Figure 28 graphs trips per day to the three nests. Inspection suggests that a line plotted for the points produced by pair (later female) 10's behavior would curve slightly beginning on about day 7. A line for female 6 would curve; frequency rose sharply at the end of the interval. It is not clear whether the data points for pair 5 produce a curve.

Several short watches on day 10 at other nests show accelerated feeding just before the young left the nest, as in the case of female 6. For example, extrapolating from a 4.5-hour observation on day 10, pair 1 increased its rate from an observed 218 trips on day 9 to a calculated 256 on day 10, both very high totals.

Nice (1943: 232) interprets feeding rates of many open-nesting passerines as revealing a "steady" increase in number of feedings per day of nest life, but some data that she summarized seem in fact to produce curves of the kind noted for female 6 (see Hann 1937: 218, Nice and Nice 1932: 102, 162; see also Cox 1960: 23, Table 9; Mayfield 1960: 102–103).

As stated, proportion of feeding trips according to sex of parent appears not to have changed as the nestling interval proceeded. If data (from Table 85) from hatching day are adjusted to exclude trips made by females before males discovered the young, males' shares of total feeding trips per day were as follows: Male 1—day 1, 45%; day 9, 35%. Male 3—day 3, 56%; day 6, 57%; day 9, 44%. Male 4—day 1, 60%; day 5, 78%; day 8, 59%. Male 5—day 2, 22%; day 6, 46%; day 7, 52%; day 9, 46%. Male 10—day 1, 57%; day 3, 40%; day 7, 35%; day 9, 0% (by day 9 this male evidently had deserted or died; he was not seen again). These percentages suggest no general pattern of variation. Proportions of male trips during my latest watches at four nests were smaller than during my earliest watches but two of the changes are slight. Further, midway through the nestling interval males 3, 4, and 5 made a higher percentage of the day's trips than they had on the first watch.

Interaction of feedings by male and female.—Females fed more frequently when unassisted than when mates were contributing parental care. Thus females 6 and 10 without help from males made about the same number of trips as did both members of the pair together at most nests when both male and female fed (Table 85). Female 6's 62 trips on day 3 are to be compared with pair 3's 59 trips on that day, female 6's 69 trips on day 5 with pair 4's 70 trips on that day, female 6's 89 trips on day 7 with pair 5's 75 trips on that day, female 6's 98 trips and female 10's 96 trips on day 9 with pair 5's 83 trips on that day (but also with pair 1's 218 trips). The most striking illustration of female 6's adjustment to her unassisted status is the contrast between her 69 trips and female 4's 19 trips, both on day 5; yet because of the contribution of male 4, total feeding trips to the two nests on day 5 differed by only 1. Bigglestone (1913) counted 278 feeding trips by a male and female Yellow Warbler on day 7 of the nestling interval; the female made 161 of these. Next day the male did not feed, and the female made 264 trips; she maintained about this rate the following day (see also Kendeigh 1952: 63; compare Nice and Nice 1932: 97–98 with Pitelka 1940: 11).

The degree to which unassisted females could extend themselves is shown by watches from 0530 to 1130 on days 10 and 11 at female 6's nest: She made 66 and 86 trips, respectively, for rates of about one feeding trip per 5.5 and 4.2 min. This latter was the most rapid rate observed for any period exceeding 2 hours. (Female 1 made one trip per 3 min in the 2 hours before her young left the nest on day 11; her mate also fed.)

In contrast to cases in which the female stepped up her feeding rate were those in which she ceased to feed or reduced her feeding. The effect on the behavior of males is suggested by daily observations at a nest (of pair 4) unusually exposed to sun (see pp. 209–210). I watched it every day of the nestling interval for at least 5 hours. Weather varied from very hot to moderate, with showers or storms on some days, and female 4's time on the nest (and consequently her feeding) varied with the weather. Between 0945 and 1420 (about 4.5 hours) on day 6,

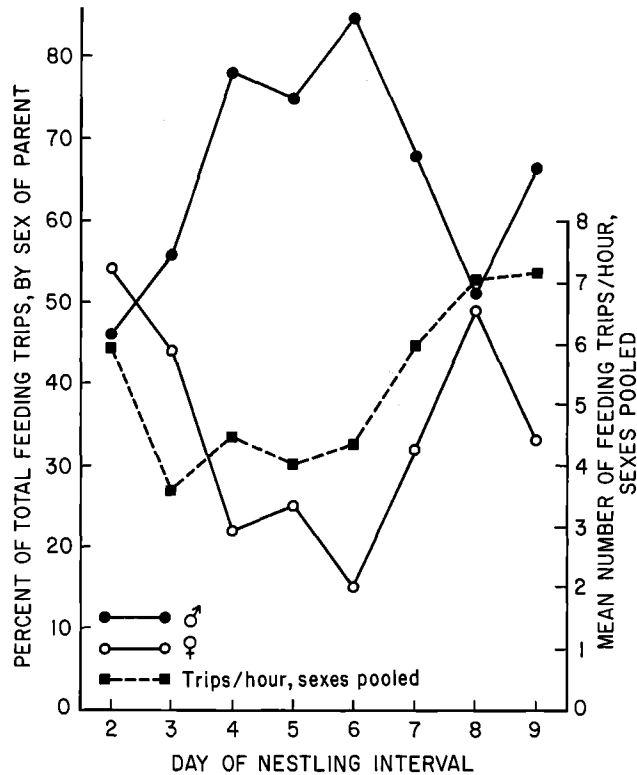


FIGURE 29. Apparent effect of exposure of nest on relative contributions of male and female to feeding of nestlings. Data are taken from the nest of pair 4 (Table 80), which was watched daily, 0800–1300. See text for details for exposure and weather.

which was hot, she left the nest only three times, for 20, 3, and 4 min; periods at the nest preceding these periods away had lasted 30, 92, and 123 min, respectively (see also her data for day 5, Tables 80 and 82, and compare with those of other females on days 5 and 6). The solution of pair 4 to the problem of feeding the nestlings while providing adequate shelter is shown in Figure 29. Hourly rates of food trips increased steadily as their young grew older, but the daily proportions of trips by male and female fluctuated greatly and, of course, reciprocally (compare Nice 1937: 131). The female's prolonged stays at the nest were probably the factor responsible for the male's increased feeding on hot days, with the intensity of the young's hunger regulating the male's rate. This case demonstrates the importance of male participation in parental care in the Prairie Warbler; in nests exposed to sun, cold weather, or chilling rain, nestlings of unassisted females would face either death from exposure or inanition. (Young that I removed from the nest to band showed immediate discomfort, evidently almost to prostration, when I held them in the sun. Once I placed two young almost ready to leave the nest in a trap well covered with leafy branches; the location was sunny and the birds died within a few minutes.)

Unassisted females that produced young may have reduced the probability of their own survival (see Welty 1962: 331, Lack 1966: 53). Female 6 brought

off three young from an unexposed nest in ideal weather. I caught her the day the young left the nest, and she weighed only 6.0 g, less than any adult caught on the study area (see pp. 544–545; compare Lack 1966: 53). For comparison, the lowest weight of 76 spring-migrant females killed in migration through Florida, presumably shortly after overwater flight from winter homes, was 5.7 g (Nolan and Mumford 1965); the mean was 6.5–6.6 g.

Frequency of feeding trips according to hour of day.—This section is based on observations of parents that fed nestlings throughout 18 full days, with the following exceptions: (1) Male 5's feeding on day 2 is included, although he probably did not discover his young until 0758. (2) I have included pair 3's behavior on day 7, when rains slightly curtailed the watch, and have arbitrarily credited the female with 2 additional feeding trips at 1900 and with 4 trips at 2000, the male with 1 trip at 1900 and 2 at 2000. (3) Excluded are all watches on hatching day except the watch at a nest (of female 10) whose first young hatched before daylight.

Feeding trips per hour are analyzed for four somewhat overlapping samples, made up as follows: (1) all 18 watches (1448 feeding trips), regardless of stage of nestling interval or sex of parent; (2) three watches of unassisted or negligibly assisted females with very young nestlings (female 10, day 1; female 5, day 2; female 6, day 3); (3) four watches of unassisted females with nestlings at least 5 days old (female 6, days 5, 7, 9; female 10, day 9); (4) eleven watches at nests where both parents fed and nestlings were at least 3 days old, with feedings plotted separately by sex.

Figure 30 shows a sharp peak of feeding trips just after dawn, the time of maximum activity, followed by a gradual decline until 1000; after this the rate changed little until an abrupt decline at 1600. The pace then rose gradually and nearly steadily until the feeding day ended. Although this suggests equal numbers of trips for intervals 1900 and 2000, the rate was in fact faster for 2000 because it lasted less than 60 min (i.e. darkness shortened it).

Hourly percentages of feeding trips of females whose behavior is graphed in Figures 30-B, 30-C, and 30-D are very similar. That is, male participation or nonparticipation apparently did not affect the hourly distribution of female trips, and the increase in number of female trips as the young grew older involved little or no change in their relative hourly distribution. Most differences suggested by curves in female behavior in Figures 30-B, 30-C, and 30-D are known to be assignable to sampling error, but one point appears worth noting: Figures 30-B and 30-C indicate that at 1600 unassisted females did not reduce feeding trips. The necessity for young nestlings to be brooded in the cooler part of the day, i.e. first half of the morning, may have prevented unassisted females from feeding them as much as they needed; if so, a deficit could have been made up in the late afternoon, when mated females normally were least attentive (see also Chapter 21 and Kendeigh 1952: 76). As for older nestlings, possibly their increased food requirements did not permit unassisted females to reduce feeding in the afternoon.

The distribution of male feedings is strikingly like that of females, except that rates of trips fluctuated more after 1600 and a lower proportion of the day's trips fell shortly before dusk. Some males brought food very actively in the intervals

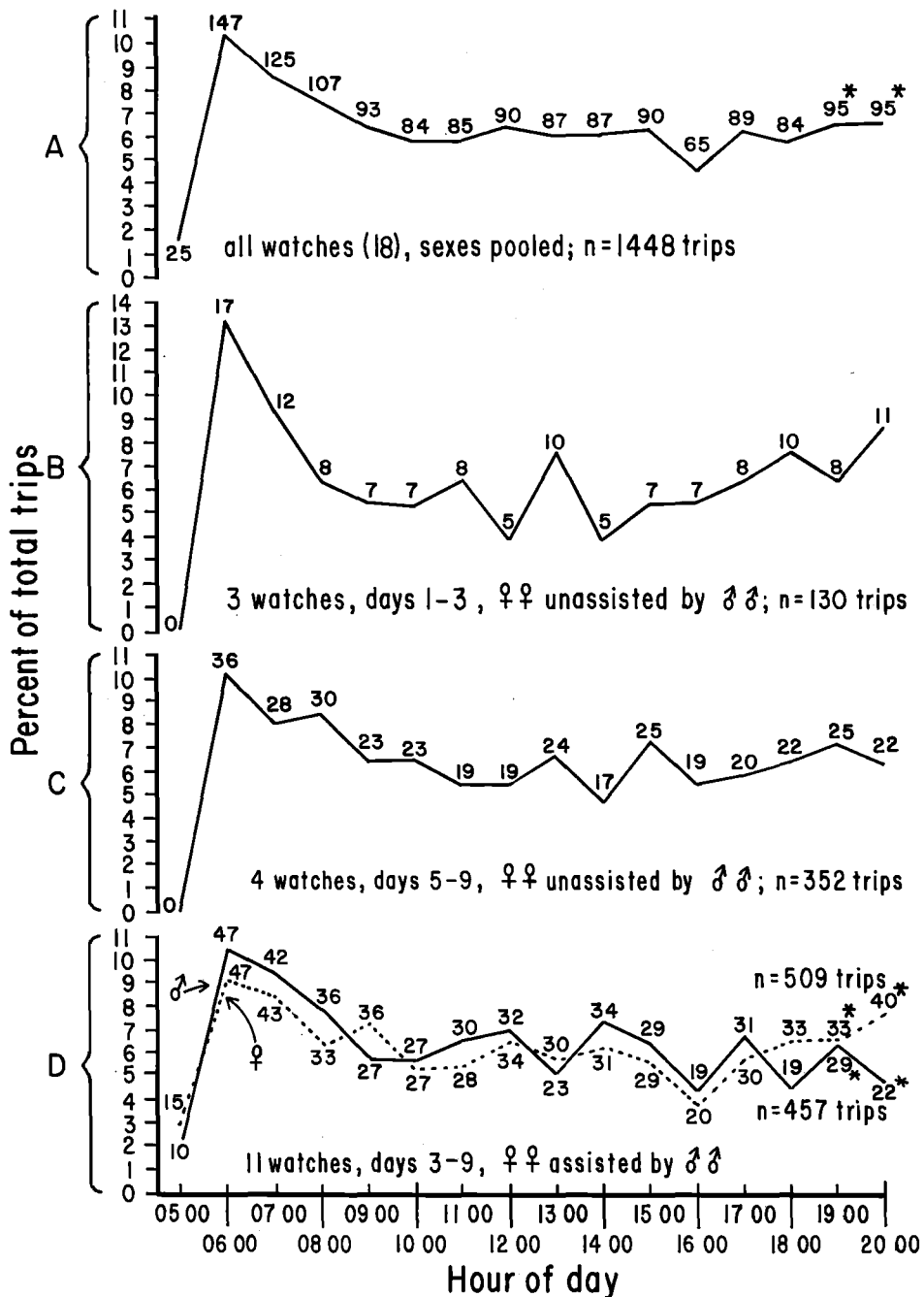


FIGURE 30. Distribution of feeding trips to the nest, according to stage of the nestling interval, hour of day, and degree of male participation. Time is eastern standard. Hours run from 30 min before to 30 min after times designated, e.g. from 0630-0730. Shown at each hour-point is the absolute number of feeding trips; * indicates numbers adjusted as described on page 265.

1900 and 2000, but others fed little or not at all (see Table 85). It is clear (Fig. 30-D) that the male's hourly schedule did not complement the female's: He did not feed more at hours when she fed less, just as he probably did not bear a heavier relative feeding responsibility early in the nestling interval when she brooded most (see above; see also Pitelka 1940).

Relationship of brood size to frequency of feeding.—Effect of brood size on number of feeding trips per day is not clear, because most data were derived from broods of three. But parents of broods of two may have made fewer trips: During 3 watches on day 3, the nest to which fewest trips were made was the one containing 2 young, as was also true on day 7 (see Table 85). However, for five watches on day 9, when frequency of feeding varied most, no such correlation appears.

Effect of weather.—The only detected effects of weather have been discussed (pp. 251, 258, 263–264).

Effect of polygyny and of presence of two broods on male's behavior.—Six males had one female with a brood of nestlings and a second female at an earlier stage of reproduction; all males fed the nestlings. I watched one of these male's nests (two nestlings) for 10 hours distributed among afternoons of days 1–9. The male fed as often as did the nestlings' mother, except on 2 days on which his other mate was engaged in active building; her building engaged his attention in the usual way (Chapter 16), but even so he fed his nestlings 5 times while their mother made 14 feeding trips. These data suggest that participation by polygynists in care of nestlings was affected by the stage of reproduction of the second mate.

No polygynous male ever chanced to have two sets of nestlings simultaneously, but some had one brood of dependent fledglings and one of nestlings. From the point of view of these males, this situation appears identical to that of monogamous males having a first brood of fledglings and a second brood of nestlings, and I have therefore pooled the few cases of these two kinds. The following are representative and indicate considerable difference in male responses to competing demands of two broods, possibly in part associated with differences in ages of the broods: (1) A male with one fledgling 35 days old did not feed second-brood nestlings during my 6 hours of observation covering 5 days. (2) A male fed newly hatched nestlings of a second brood while still giving food, at least occasionally, to a first-brood fledgling 53 days old (an unusually long period of dependence; see Chapter 28). (3) A male probably quit caring for two first-brood fledglings when they were about 35 days old (an unusually short period of dependence) and fed nestlings. (4) A polygynous male fed both broods for at least 1–2 days; by the time the nestlings were 8 days old he had apparently abandoned two fledglings 38–39 days old. When one begged for food as the male went to the nest, the male flew at the fledgling and supplanted it. The fledgling disappeared next day. (In an almost identical case the male was monogamous, with two broods.) (5) A polygynous male with one fledgling devoted himself almost entirely to its care. I watched nestlings 1 hour per day for 8 days and saw the male feed them only twice on day 6 and once on day 8 (when the fledgling was 32 days old).

As for allocation of feeding by females whose first broods were still dependent when second-brood nestlings were present, once I probably saw a female with

TABLE 86
PERIODS BETWEEN TRIPS TO NEST WITH FOOD DURING DAY-LONG WATCHES,
ACCORDING TO SEX OF PARENT AND DAY OF NESTLING INTERVAL

Day ¹	Individuals N	N	Periods			
			Length, min			
			Mean	SD	C ³	Median
Females						
1	5	117	22.1	15.0	0.68	19
2	1	34	26.1	18.9	0.73	22
3	3	117	22.6	18.2	0.81	16
5	2	86	20.5	19.5	0.95	15
6	2	58	29.9	18.1	0.60	26
7	3	166	18.7	14.7	0.78	15
8	1	46	19.2	17.9	0.93	14
9	5	428	10.2	11.2	1.10	7
Totals	7 ²	1052	17.1	13.8	0.81	
Males						
1	3	49	19.3	16.5	0.86	18
2	1	9	64.8	91.2	1.41	30
3	2	52	33.6	25.5	0.76	26
5	1	50	17.7	13.0	0.74	14
6	2	62	23.9	21.7	0.91	19
7	2	61	27.1	17.9	0.66	23
8	1	66	13.1	13.5	1.03	11
9	3	152	16.8	15.3	0.91	13
Totals	6 ²	501	21.4	20.8	0.97	

¹ The day the first young hatched, hatching day, is day 1, etc.

² All watches were carried out at the nests of 7 females. One had no mate during the full nestling interval; one apparently lost her mate between days 7 and 9.

³ C is the coefficient of variation.

nestlings give food to begging fledglings; but in general (cases were few) such females probably fed only the nestlings.

Length of periods between feeding trips.—Table 86 shows periods between feeding trips, according to sex and day of nestling interval, during the 22 day-long nest watches. For both sexes periods tended to shorten as the interval advanced, but the trend is considerably clearer for females. On 4 of the 8 days of the interval on which watches were carried out, mean and median times between trips by females were longer than those for males; data pooled for the full interval and according to sex do not differ.

Nice (1930a) states that both sexes of the Black-throated Blue Warbler feed in little bursts of activity, with longer intervals in between (compare Kendeigh 1952: 68), but I found no such spacing of trips by Prairie Warblers.

Duration of stay at nest in connection with feeding.—Table 87 presents, for each sex, frequency distributions of length of stay at the nest per feeding trip, including time devoted to disposing of any feces, during day-long watches. Unit intervals are of unequal length in order to simplify summarizing a few long stays. All distributions are positively skewed, as indicated by differences between medians and means. Data are segregated according to day of interval, except that the single watch on day 2 is pooled with watches on hatching day and the single watch on day 8 is pooled with those on day 7. Because females often remained and brooded, shaded, or perched after feeding whereas males did not behave in this

TABLE 87
PERIODS SPENT AT NEST FEEDING,¹ ACCORDING TO SEX OF PARENT
AND DAY OF NESTLING INTERVAL

Length, sec	Day of Interval ^{2,3}											
	1-2		3		5		6		7-8		9	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1-10	22	—	6	1	9	11	38	6	50	44	115	225
11-20	15	—	12	2	11	6	6	7	28	43	17	68
21-30	5	—	7	7	5	6	9	2	13	23	2	21
31-60	5	—	9	4	13	3	2	0	17	21	3	44
61-120	4	—	9	2	8	0	1	3	4	7	4	20
121-300	6	—	6	1	1	1	1	0	1	0	2	6
Total	57	—	49	17	47	27	57	18	113	138	143	384
Median	15	—	29	28	30	14	10	15	15	14	8	10
Mean	32	—	60	51	41	24	19	31	22	25	14	21

¹ Periods were measured with a stopwatch, from arrival at the nest to departure, but some measurements are approximations. Some periods were not measured. Periods of females were counted only if the females did not remain and brood or shade. Early in the nestling interval, females that brought food usually brooded after feeding.

² The day the first young hatched, hatching day, is day 1, etc.

³ Data from days 1 and 2 and from days 7 and 8 are pooled because of the few cases on day 2 and day 8

way, I tabulated only female stays that were not followed by brooding-shading; for males all stays were tabulated.

Variation in duration of stay at nest according to day of nestling interval.—Length of stay did not vary according to sex. Both adults tended to shorten stays as the interval advanced. As nestlings grew they swallowed food more easily, eliminating need for repeated delivery of the same item. Associated with the many trips of some parents on day 9 and thereafter was a change in general demeanor; these birds seemed to rush to and from the nest, and all leisurely pauses were eliminated.

Variation in duration of stay at nest according to hour of day.—Most longer stays were at midday or in the afternoon, when the pace of feeding was least intense. But analysis of all stays of selected individuals observed during full days shows no significant difference according to 4-hour intervals from 0430 to 2030.

FOOD OF NESTLINGS

Taxa and sizes of items.—I could determine the class or order of 761 arthropods delivered to nestlings during day-long watches. Caterpillars numbered 622 (82%), about 550 of them green; most were 20–25 mm long, but some were 50 mm. Insect imagoes or nymphs accounted for 121 items (16%); I recognized 9 moths, 8 flies, 3 orthopterans, a few bugs and wasps, and 1 damselfly. Seventeen spiders (2.2%) and one millipede were identified. Percentages doubtless were biased by differences in the ease with which groups could be recognized at a distance.

Males and females did not appear to differ with respect to taxa of prey brought. Changes in size (from very small to large) were evident as the nestling interval advanced. At its beginning males generally brought larger items than females, but an occasional male consistently did the opposite (on day 5). Later, with one exception, I noticed no sexual difference in this respect; the exceptional male brought much bigger items than his mate did. Nice (1943: 233) cites a number

of studies, most of parulids, in which males are reported to feed larger objects to nestlings than do females.

Numbers of items brought and of nestlings fed per trip.—Number of items brought was probably correctly determined on 780 feeding trips as follows: 1 on 574 trips (74%), 2 on 193 trips (25%), 3 or more on 13 trips (2%). The sexes did not differ. Number per trip seemed to change as nestlings grew older. I never saw more than 1 item brought on hatching day, but on day 7 more than 1 was brought in 27 instances. By day 9 some adults fed so often they probably had no time to find two insects between trips.

On 1558 feeding trips I knew the number of nestlings that received food: 1 on 1434 trips (92%), 2 on 118 trips (8%), 3 on 6 trips (< 1%). Most (85%) of this information was obtained on day 5 or later, when nestlings raised their heads high enough to permit feeding to be seen. Food brought by males was distributed to more than one nestling significantly ($P < 0.05$) more often than food brought by females, but probably only because males sometimes passed part of their food to females to deliver (see Chapter 25).

In at least 90% of the cases, the nestling fed was the one whose head was highest or was one of several equally high. Position relative to the adult's perch conferred no advantage. Distribution of food by one parent to more than one nestling usually occurred when a recipient began to swallow immediately, leaving the adult with food undisposed of. Adults sometimes held items so far back in the mouth that it took a moment to produce them; during the delay any young that had already received food swallowed it and at times subsided into the nest, and remaining items when ready were passed to another nestling. Occasionally adults seemed almost to regurgitate; a female moved her head as though in an effort to dislodge food from far down in the mouth (compare Wheelock 1905; see Andrew 1961).

Number and rate of meals of young per day, according to day of nestling interval.—To estimate number of meals per nestling during day-long watches (Table 85), I assume on the basis of the preceding subsection that on hatching day 1.0 nestling was fed per trip and that thereafter the number was 1.1 nestlings. Calculation of number of meals on hatching day is only for the first individual that hatched; this bird received all meals brought until the second young hatched, then is credited with half the meals until the third hatched, etc. My only watch on day 2 began while one of three eggs was still unhatched. I calculated only the meals of the two nestlings present all day, proceeding as just described for the first young on hatching day.

For the feeding rate, I divided calculated number of meals per young into 900 min. This interval was selected for simplicity and because it is about the length of the mean active and mean feeding day (p. 244). For meals on hatching day, the rate was determined from time of hatching at the various nests until 2030. Occasional meals were rejected by young apparently because they were sated or could not swallow items of the size offered. No adjustment for this is made in Table 85; such cases were few and probably not all were seen by me.

Considering the previous discussion of numbers of feeding trips, only a few comments on numbers of meals (Table 85) are necessary.

1. On hatching day the mean rate of feeding of the first young was faster than

mean rates per individual on days 2–6 and was not exceeded until day 7. This probably reflects what appeared to be excitement of some adults when hatching began. That it is not entirely attributable to the first nestling's appetite is suggested by the subsequent drop in rate when nestling size was increasing (see Chapter 26). As an illustration of apparent excitement, a male after first seeing its nestling made six feeding trips in 15 min and during this period twice went to the nest without food and looked at the young.

2. Although numbers of meals per day changed very little between day 2 and day 6, food items became progressively larger during at least part of this time, as already noted.

3. From day 7 onward meals per nestling per day varied greatly from nest to nest. On day 9 the 3 nestlings of female 1 were given food at a rate 2.5 times faster than the 3 of female 5. However, a difference in sizes of meals may have compensated for this reduced frequency, as is suggested below by data on frequency of defecation by these two broods (see below).

NEST SANITATION

Behavior of nestlings when defecating is treated here rather than in Chapter 26 (which deals with other nestling behavior), because it cannot be separated conveniently from the subject of nest sanitation. Color terms are not based on a color chart.

Description of feces, defecation.—Feces were difficult to observe early in the interval; usually they appeared to be 3–4 mm in diameter, brownish or blackish, sometimes watery, not noticeably encapsulated. From day 3 onward feces were whitish and enclosed in a gelatinous capsule with a greenish-black area at one end. Fecal sacs after day 4 or 5 probably did not vary in size according to age of nestling (compare Eaton 1958, Mayfield 1960: 111); a sac excreted on day 5 weighed 180 mg; sacs from two birds on day 6 weighed 150 and 200 mg; sacs from two birds on day 7 weighed 170 and 200 mg.

Defecation usually was not observable until young were large enough to rise above the nest rim. From day 5 or 6 and increasingly thereafter, nestlings raised the anal region before defecating, sometimes after wriggling to shake free of nest mates. After the anal region had been elevated as high as or higher than the head, typically it was turned partly toward the parent and then moved slightly from side to side while the sac emerged. Large nestlings at times thrust the vent far toward the side of the nest and defecated on or over the rim. Time required to defecate depended at least in part of the time necessary to free and raise the body; usually it was 2–3 sec.

Stimulus for defecation.—Of some 500 recorded cases of nest sanitation, all but 6 followed feeding. Normally 2–6 sec elapsed after swallowing (probably with no variation according to day of nestling interval), but sometimes 15–30 sec passed; during longer waits frequently the parent touched the nestling lightly with its bill, apparently near the anus (compare Mousley 1924: 269). Mayfield (1960: 104) reports that Kirtland's Warblers peck at the nestling's bill and stimulate defecation; I saw one male Prairie Warbler touch the bill of a nestling four or five times after it had swallowed.

TABLE 88
NUMBER OF DEFECATIONS BY NESTLINGS DURING DAY-LONG WATCHES

Pair or female ¹	Day of nestling interval ²	Brood size	Defecations		
			Total	Mean/nestling	Mean/nestling as % of meals/nestling ³
4	5	3	25	8.3	33
6	5	3	26	8.7	35
5	7	3	26	8.7	32
6	7	3	34	10.7	33
4	8	3	35	11.7	29
1	9	3	43	14.3	18
3	9	2	22	11.0	22
5	9	3	31	10.3	34
6	9	3	38	12.7	35

¹ Numerical designations are those applied to these same females in Table 66 and Chapter 21.

² The day the first young hatched, hatching day, is day 1, etc.

³ Meals per nestling are presented in Table 85.

My picking up nestlings often caused them to defecate (see also Schrantz 1943: 381), most frequently after day 5 when they were becoming conscious of their surroundings (Chapter 26); fright rather than (added to?) touch may have caused defecation. Nestlings 6 days old that had defecated upon being picked up could repeat the process in about 15 min and again in about 10 min; the first sac was normal; the second was a small, gelatinous capsule; the third was also small and was watery and not encapsulated.

Three times young defecated not after eating but during the female's period at the nest; the sacs were carried away. Doubtless I overlooked other such cases because sacs were small and were eaten (see below). Three large nestlings defecated on the nest rim between feedings when no adult was present; the sacs were removed by the next parent to bring food.

Time of first and last defecation of day.—Eleven times on days 5–9 (without apparent variation according to day) I observed the first defecation of the day. The earliest time was 0508, the latest 0629 (33 min later than the second latest); the mean was 0542.5 (SD 24.8 min), the median 0537. Intervals between the female's first leaving the nest (or going to it, if she had spent the night elsewhere) and the day's first defecation ranged between 5 and 76 min; the mean of 11 cases was 20.0 min (SD 21.2 min). On 3 mornings, the first defecation occurred after the first feeding, on 3 after the second feeding, on 3 after the third, on 1 after the sixth, on 1 after the seventh (but only 17 min after the first feeding trip).

The final defecation of the day was at 1939 in the earliest case, 2015 in the latest; the mean of 10 cases was 1950.5 (SD 12.4 min). No variation according to day (5–9) of nestling interval was evident.

Frequency of defecation, days 5–9.—I obtained probably complete data on frequency of defecation during 9 day-long watches from days 5 through 9. (Prior to day 5, feces often were eaten while parents' bills were out of sight; also, it was often impossible to tell whether an adult was taking back food and softening it or disposing of feces.) Numbers of defecations per nestling increased daily, from 8.7 on day 5 to extremes of 10.3 and 14.3 on day 9 (Table 88).

TABLE 89
FREQUENCY OF NESTLING DEFECATIONS DURING 9 DAY-LONG NEST WATCHES,¹
ACCORDING TO HOUR OF DAY

Hour ²	Defecations		Number of defecations as % of nestlings present (nestlings = 26) ³
	N	% of total	
0500	1	0.4	4
0600	28	10.0	108
0700	23	8.2	88
0800	20	7.1	77
0900	21	7.5	81
1000	15	5.4	58
1100	15	5.4	58
1200	18	6.4	69
1300	20	7.1	77
1400	15	5.4	58
1500	19	6.8	73
1600	11	3.9	42
1700	21	7.5	81
1800	13	4.6	50
1900	22	7.9	85
2000	18	6.4	69
Total	280	100.0	

¹ The 9 watches are those analyzed in Table 88; see the data there.

² Hours began 30 min before and ended 30 min after the times used to designate them; e.g. 0700 is the period 0630–0730.

³ Each nestling is counted once each day it was present; during 8 watches brood size was 3 and during one watch, 2.

Relationship of frequency of defecation to frequency of feeding.—Between days 5 and 9, when the nine nest watches referred to in the preceding paragraph were made, number of feedings per day increased. Data for seven of those same 9 days show a rather constant relation between frequency of defecation and frequency of eating: mean number of defecations per nestling per day was from 29% to 35% of mean number of meals (Table 88). On 1 day frequency of defecation was only 18% of frequency of meals, but feeding trips were much more numerous than on other watches (Table 85, pair 1, day 9). Assuming that rate of defecation is a function of both frequency and size of meals, this evidence suggests that the nestlings of pair 1 on day 9 received less per meal than nestlings fed at a slower rate (compare Mayfield 1960: 102–103).

Frequency of defecation, according to hour of day.—Table 89 shows absolute and relative hourly distributions (see p. 207) of the 280 instances of nest sanitation on the nine day-long watches dealt with in Table 88. Total nestlings numbered 26, counting each bird once each day it was observed.

Defecations were most numerous in the interval 0600, the first full hour of activity. They then decreased nearly steadily until 1000, fluctuated somewhat until 1500, and fell to their lowest point at 1600. At 1900, just before dark, they were as frequent as at 0700. A curve (not shown) drawn from the data in Table 89 considerably resembles the hourly curve of feeding trips (Figure 30).

Shortly after waking in the morning and being fed, nestlings probably voided excrement from food eaten late the preceding day. Thereafter the proportion of defecations per hour was doubtless dependent not only on the amount of food eaten in the immediately preceding period but also on the rate of feeding during the current hour (because, as noted, feeding and associated adult behavior stimu-

TABLE 90
METHOD OF DISPOSAL OF FECES, ACCORDING TO SEX OF PARENT
AND DAY OF NESTLING INTERVAL

Day ¹	Male			Female		
	Sacs eaten	Sacs carried away	% carried away	Sacs eaten	Sacs carried away	% carried away
1-2	2	0	0	23	0	0
3-4	14	3	18	34	8	19
5-6	6	40	87	14	34	71
7-8	8	42	84	8	65	89
9-11	2	51	96	8	129	94

¹ The day the first young hatched, hatching day, is day 1, etc.

lated defecation). Cox (1960: 21-22) reports that Mourning Warblers feed least often early in the day and that fewer fecal sacs are produced at that time.

Adult disposal of feces, according to day of nestling interval and sex of adult.—Feces were sometimes eaten, sometimes carried away. Table 90, based on all nest watches that lasted at least 4 hours, distributes cases between these two methods according to 2-day segments of the nestling interval and also sex of parent. All feces were eaten on the first 2 days of the interval. On days 3 and 4 both parents carried a few sacs away, after which that method greatly predominated (compare Walkinshaw 1959). Males and females did not differ.

Proportions of sacs disposed of by each sex, according to day of nestling interval.—All adults appeared strongly motivated to dispose of feces and often seemed to compete for sacs (even trying to catch in mid-air any voided over the rim of the nest). Females had greater opportunity to dispose of feces and did so somewhat more than males because (1) females often remained at the nest when males brought food, especially during days 1-3, whereas males usually were absent when females brought food; and (2) males seemed to let females dominate affairs at the nest, particularly early in the interval.

On days 1-3 at 6 nests, males disposed of only 6 (11%) of 52 sacs. On day 4 males at 3 nests disposed of 26 (57%) of 46 sacs; but on 53% of male feeding trips, females were absent from the nest, an unusually high percentage for that day of the interval (see Chapter 25). During the remainder of the interval, percentage of sacs disposed of by each member of the pair varied greatly from nest to nest.

As expected in view of the fact that defecation almost always followed eating, the individual parent's contribution to nest sanitation may have been positively correlated with its proportion of feeding trips. The following compares proportions of female feeding trips and acts of nest sanitation on the day-long watches on which Table 88 is based (omitting data for the unmated female 6); percentage of feeding trips is given first, and semicolons separate data for different females: 22%, 15%; 48%, 62%; 28%, 41%; 65%, 72%; 56%, 25%; 54%, 48%.

Factors affecting nest sanitation by female.—Females that spent a high proportion of time at the nest tended to eat sacs, which probably explains why eating predominated as the disposal method early in the nestling interval. Female 4, whose very exposed nest has been discussed above (e.g. on p. 263), ate sacs

more often than other females: On day 8, she was at the nest an unusually large share (44%) of the day and disposed of 10 sacs, 7 by eating.

Details of disposal by carrying.—Most sacs were probably carried off the territory; I saw none dropped or put down within 35 m of the nest. One female invariably carried feces across 35 m of shrubland that separated her nest from a mature woods, entered the woods and was lost to view when well beyond normal Prairie Warbler habitat. Both members of one pair carried many sacs off the territory and into or beyond an adjacent grain field; usually they crossed this field to a tree row 135 m from the nest, but at times the male dropped sacs in midair into the field. Another male repeatedly carried sacs to large trees 80 m away and not within any Prairie Warbler territory. However, Walkinshaw (1959) saw parents carry sacs only 6 and 15 m from a nest.

Opportunities to observe details of disposition of sacs that were removed were rare because they were carried far, as just described. Of about 40 observed dispositions, the sac was dropped in flight in 7 and in the rest placed on a branch or (occasionally) dropped from a perch after the parent had alit. All but two cases of dropping in flight were performed by a single male; the fact that most birds carried sacs into woods or clumps of trees suggests that such dropping was uncommon. Birds sometimes wiped the bill after disposing of sacs.

Most flights were at a height of about 2 m until the carrier approached the point of disposal, when it suddenly gained altitude, landed at 4–10 m, and put the sac on a branch or dropped it. Some individuals developed habits as to the route followed, narrowing their already limited range of pathways in leaving the nest (p. 276) and carrying sacs to only two or three areas for disposal. The precise point at which the sac was deposited or dropped was probably randomly chosen from trip to trip.

CHAPTER 25

BEHAVIOR OF ADULTS DURING THE NESTLING INTERVAL

BEHAVIOR IN CONNECTION WITH FEEDING YOUNG

Movement to and from nest.—Behavior of both males and females in trips to and from the nest was very much like that of females during incubation (Chapter 22), and only behavior that differed will be mentioned.

Males tended to approach more slowly and gradually than females, usually landing 20–30 m from the nest and singing 1–3 min before going to it (see below). Song perches were 4–8 m high and elevated above surrounding shrubs; after singing males often dropped down and made two or three more stops enroute to the nest. An occasional bird stayed almost at ground level during his final approach, hopping through low growth in what may have been cryptic behavior. Hann (1937: 180–181) found that the female Ovenbird goes quickly to the nest and the male more slowly, as in the Prairie Warbler.

Both sexes developed distinct directional preferences for departure, sometimes using the preferred direction 75% of the time; members of a pair often had different preferences. Females usually flew directly and quickly away; males unless carrying feces were more likely to hop about in the nest tree 15–20 sec, at times returning to glance at the nestlings, then to depart in short flights. Sometimes males paused to sing.

Foraging area.—Foraging exploited the whole territory; both sexes were often observed gathering food at least 50 m from the nest. Toward the end of the nestling interval, females making very frequent feeding trips (see p. 263) probably usually foraged closer than 50 m; some darted rapidly back and forth to the nest, often catching food only 5–10 m from it. Males' feeding rates tended to be slower than those of females (see Chapter 24); males never foraged systematically near the nest.

Preparation and delivery of food.—Adults prepared food for nestlings as for themselves (see Chapter 39) but often softened it more thoroughly. A parent sometimes took an insect back five or six times because a nestling did not swallow it immediately; having retaken it, the adult usually moved it back and forth across the bill while squeezing it, then delivered it again, frequently to a different nestling. Rarely, items not eaten readily were carried away or eaten by the parent. When both adults were at the nest, one sometimes withdrew food from a nestling's mouth as soon as the other had delivered it, often passing it to a different nestling. Living, apparently untreated caterpillars were at times fed to larger young.

The method of grasping caterpillars to be delivered differed according to their size. Usually those 5–20 mm long were grasped about in the middle and thrust into the nestling's mouth, but larger caterpillars were held behind the head and inserted headfirst (compare Ficken 1962b). Adult insects, nymphs, and spiders were held by the thorax or abdomen.

Positions while delivering food.—Soon after the eggs hatched nearly all adults

TABLE 91
REACTIONS OF FEMALE TO ARRIVAL OF MALE AT NEST WITH FOOD,
ACCORDING TO DAY OF NESTLING INTERVAL

Day ¹	Present when male arrived									Totals
	Absent when male arrived		Arrived simultaneously with male	Left nest		Remained				
						Took and delivered food	Rose, let male deliver food	Already on rim, let male deliver food		
N	% ²		N	% ³	N	% ³				
1–2	24	32	1	21	42	27	54	2	0	75
3	18	23	2	20	35	22	39	10	5	77
4	28	53	1	6	25	15	63	2	1	53
5	29	39	1	22	50	21	48	1	0	74
6	44	45	4	20	40	15	30	8	7	98
7	67	68	5	12	44	11	41	4	0	99
8	57	60	5	21	64	12	36	0	0	95
9–10	154	70	17	28	56	7	14	1	14	221
Totals	421	53.2	36	150	44.8	130	38.8	28	27	792

¹ The day the first young hatched, hatching day, is day 1, etc.

² Percentages are based on total feeding trips shown in the right-hand column.

³ Percentages are based on totals in the right-hand column minus (a) number of occasions when the female was absent when the male arrived and (b) number of occasions when the female arrived simultaneously with the male.

formed a preference for a particular perch (on the nest rim or a twig) from which to deliver food and used it nearly exclusively thereafter. Members of a pair usually did not have same preference.

Reactions of female to arrival of male at nest.—The male's song before going to the nest appeared to alert the female, if she was there (see below); the disadvantage of arriving unexpectedly and surprising the female seems clear. Female reactions varied; Table 91 (based on nest watches lasting at least 1 hour) shows these. The male's arrival (occasionally, his beginning to sing nearby) often caused her to leave, possibly having this effect more commonly as the young grew older (Table 91); other females remained and watched or helped the male feed.

When the female left at the male's arrival, his flight into the nest tree at or near nest level and her emergence on the opposite side of the tree, also at nest level, were at times perfectly synchronized. An observer might think he had seen one bird moving through the tree and follow the female from the vicinity of the nest (compare Van Fleet 1919; Bent 1950: 364-365). While such synchrony would appear to be a valuable diversionary mechanism, it occurred in fewer than half the cases. The female sometimes left before the male's arrival, and flight speeds of the arriving male and departing female often differed too much to be deceptive.

The female's departure may have made the male more willing to go to the nest; agonistic motivation between the two was apparent at times. Gaping was not uncommon when the pair were together at the nest; two males left nest trees without feeding when females were present and returned after the females left.

When the female stayed at the nest, the male often passed all or part of his food to her and she relayed it to the young, especially early in the nestling interval (see Table 91). Behavior in passing food varied greatly. Occasionally a male

offered an item to the female several times; sometimes the female turned her open mouth toward him but received food only after a pause, as though he were reluctant. Sometimes the female seized items from the male. Usually the exchange was quick and well coordinated.

Two females repeatedly quivered their wings slightly while watching males approach (hatching day through day 8). Generally the behavior began 5–10 sec before the males arrived at the nest but once lasted 10 min while a male sang nearby. Quivering became most intense just as the food was placed in the female's bill, as it was in 15 of 16 cases when females remained at the nest and quivered; the behavior was reminiscent of begging by fledglings (Chapter 28). Sight of the male approaching with food may have stimulated a response appropriate to an earlier stage of the female's life, and quivering may have helped induce the male to pass his food. Compare Gabrielson (1922), Mendall (1937), Cox (1960: 21); see Andrew (1961: 341), who suggests that courtship feeding in some species may have evolved from episodes like these. Twice females quivered their wings but flew just as the males arrived.

Reactions of male to arrival of female at nest.—Males that were at the nest when females arrived almost invariably flew away immediately, unless they had not delivered their food. In the latter event, males usually ignored females or reached out to take the items they had brought (but never obtained it; compare Walkinshaw 1959). When the pair was at the nest and finished feeding simultaneously, they flew away together, the male usually behind.

Walkinshaw (1959: 58) reports apparent allopreening in the Prairie Warbler: A pair was perched on the nest after feeding, and "each parent picked gently at the other's feathers then swallowed, as though eating ectoparasites."

POSITIONS OF FEMALE ON NEST

Female positions in or at the nest were about the same as during incubation (Chapter 22). Tiny young could be and usually were fully covered, although when standing directly above a female I could sometimes see heads of nestlings in the gap between her sides and the nest wall. It became increasingly impossible for the female to sit deep in the nest as the young grew, and brooding of large young appeared to consist of holding the rim with the feet, flexing the heels, and leaning as far forward onto the nestlings as possible. Brooding females apparently sometimes used their feet to adjust positions of small young. The characteristic shading position, not seen during incubation, consisted of flexing the legs so that the tarsometatarsi formed an acute angle to the tibiotarsi; the belly almost rested on the nest rim (like the position commonly seen in perched fledgling passerines).

MOVEMENTS ON OR AT NEST, OTHER THAN FEEDING

Removing invertebrates.—Males and females picked occasionally at the nest and nestlings and appeared to swallow. At certain nests this behavior was unusually frequent. I later obtained one of these and found it very heavily infested with the mite *Ornithonyssus sylviarum* Canestrini and Fanzago; the fledglings had scabby lesions on their feet, possibly the result of bites (see Chapters 33 and 38).

Once both adults devoted much time to removing what probably were ants (compare Mayfield 1960: 104–105). They began suddenly to pick at the cavity and outer surface of the nest and several times moved upward and downward from it, picking at the tree trunk. One hour later I found a few small black ants and one red arachnid on the nest. The brood in another nest probably left it prematurely because of ants (see p. 302).

Removing dead nestlings.—Dead nestlings present on one day always disappeared by my next inspection, but disposal never was observed. Harding (1931) saw a female Black-throated Blue Warbler “aided by the male” eat a dead newly hatched young.

REACTIONS TO INTRUDERS; DISTRACTION DISPLAY

Diversionary behavior observed during building (p. 142) and incubation (p. 225) continued into the nestling interval. Females that discovered me just as they were about to take food to the nest sometimes flew straight through the nest tree without pausing, then turned and called. Both sexes showed slightly increased apprehensiveness shortly after hatching; this was especially noticeable in males because of their earlier apparent lack of concern. Some individuals, particularly females, showed more intense fear reactions (e.g. calling) when the young reached age 6–7 days, and this fear continued to mount (compare Odum 1931). Distraction display became common.

Except when specified, no sex-specific behavioral difference was noted. For clarity, positions and movements of the body are first described for a perching bird, although usually displays were associated with motion through space; such motion is analyzed separately. Intensity of display varied; for convenience arbitrary levels are described.

Positions and movements, excluding locomotion, during distraction display.—Low intensity: When a bird went slowly into its display or when display remained at low intensity, progressive involvement of parts of the body could be noted. Often the first movements were a slight extension of the wrists and vibration of the wings, sometimes one wing before the other. Wings extended farther as intensity increased. Coinciding approximately with onset of wing quivering (once before it), the back was hunched slightly and the bird leaned forward so that the body was horizontal and crouched, legs and feet flexed, head lowered. Irregular Tsip calls were usual.

Medium intensity: As display became more vigorous, the wings were extended slightly more than half open and elevated 10–15° to form a wide-angle V over the back. Quivering continued, the wings traversing an arc of 30–40°; occasionally a bird held its wings motionless 2–5 sec. Hunching the back and depressing the head were more pronounced and were made more conspicuous by fanning and lowering the tail. The tail's width at its tip and the angle of its depression appeared correlated with the level of excitement; widths of 40–50 mm and angles of 45° from the line of the back were typical. Chek calls usually were commoner than Tsips, growing louder and more frequent with increasing excitement; their rate was about 2/sec. Intermingled Cheks and Tsips produced a confusing and

ventriloqual effect, as if two birds were calling. Surprised adults Sputtered when they began the display.

Maximum intensity: Vibrating, fully extended wings were held straight out to the side and almost always beat downward from the horizontal position; sometimes beats of large amplitude raised wings above the horizontal. Depression of the head and tail was so great that the line of the head formed an angle of 70–80° with the line of the back; the tail in extreme cases was at nearly 90° from the line of the back and was widely fanned, its distal end forming an arc of some 130°. Chek calls were very loud, at peak excitement forming a brief burst of continuous sound. Once a male displayed at maximum intensity but silently.

Locomotion during distraction display.—Flight was common during low-intensity and moderate displays, but the effort to hold parts of the body in the display positions impaired the ability to fly. Flights at low intensity, e.g. from the nest at my approach, could cover at least 20 m, usually with progressive loss of elevation until the bird alit on or near the ground. Wing beats were shallow, wings stiff, air speed slow; the hunched back and depressed tail caused the body to be tipped downward posteriorly. Very excited birds on high perches sometimes glided toward the intruder on outspread wings, which probably moved slightly. Deviation from normal flight increased as alarm increased; high-intensity display probably made flight impossible, and birds usually perched or, if they progressed, did so on foot. Once a female flew rapidly from spot to spot on the ground, displaying each time she landed; her progress resembled bouncing.

In one situation display in flight was nearly invariable, viz. when a fledgling that had been perching cryptically suddenly called noisily and flew in alarm. As the young launched into the air, the adult flew to it, trailed close behind it in slow display flight, then dropped to the ground between the source of alarm and the escaping fledgling. I found it difficult to avoid watching the falling adult (compare Morse 1969) and to separate its loud burst of Chek calls from the fledgling's calls. The display added greatly to my difficulties in capturing young.

Moving, displaying birds used the feet (and wings) in three different ways, sometimes switching from one way to another. The distinctions are based largely on the direction of the displayer's progress: (1) Horizontal crawling was frequent at all intensities. Birds moved slowly and laboriously over the ground or along an approximately horizontal branch, seeming to crawl or creep. As intensity of the display grew, the apparent difficulty of movement increased; the stiffly fanned and depressed tail probably really impeded advance (compare Grimes 1936). Observation of the feet was difficult, but they seemed to move alternately (compare Mayfield 1960: 64); progress was so slow and creeping that it is unlikely birds were hopping with both feet. The wings quivered. A female that crawled on the ground in thick vegetation caused conspicuous movement and rustling of plants without being visible herself; at times creeping birds made a clattering or rattling noise, probably by brushing the moving wings on vegetation. (2) Downward tumbling seemed most common in intermediate- and high-intensity display. The bird fell vertically down the trunk of a small tree or forb from a height of 1–2 m (maximum 2.5 m), often ending with a short diagonal glide to the ground. In this movement, first the body tipped far forward (the depressed tail, usually

perpendicular, now became almost horizontal), and then the bird dropped to a twig just below; its feet grabbed and momentarily held this perch but then released, causing another short fall; the falling progress was interrupted and irregular, and the body's position tended to change so that first the head was lower than the tail, then the opposite. At any time during the fall, the bird might perch and fan its wings, holding the tail nearly perpendicular; or it might leave a perch and glide to the ground. Upon reaching the ground it usually flew up to a plant again almost immediately and repeated the display, doing so five or six times. Obviously, falling from an elevated perch made the display very conspicuous. (3) Some displayers sidled along a branch with the long axis of the body at an angle of 45–90° to the line of the branch. They appeared to step with one foot at a time; the tail usually hung nearly straight down over the branch, and the body was sometimes almost at a right angle to the tail. Sidling was uncommon, appearing in displays of moderate to high intensity.

Distances involved.—Even unusually excitable adults displayed only when an intruder was near a young bird or the nest. The maximum distance separating me and a fledgling when a parent began to display was 25 m; I had hissed, which usually intensified alarm. A female that regularly showed much alarm near the nest appeared to ignore me when I was 40 m from it. Even after young had left the nest, displays were more intense near it than elsewhere. To illustrate, when I banded nestlings close to her nest, a female displayed intensely; I then took them to an adjoining territory, the female following and feeding them there but ignoring me; I then restored them to the vicinity of the nest, and she resumed intense display.

The distance to which displaying parents approached me depended on their level of excitement. In high-intensity display when I held calling fledglings, parents flew quickly to within 1.5 m of me, then moved (displaying) 4–5 m away from me, stopped, and continued to display (less intensely) 5–10 m from me. If the young called again, the foregoing was repeated. If I followed a displayer and was not holding its young, it moved about 4 m ahead of me, its speed determined by mine. Usually, when I was some 20 m from the young whose danger had caused the alarm, the display ceased and the adult only called Chek or Tsip.

Females that flew from the nest in display flight generally permitted an approach to within 2–3 m before they left, then flew 8–20 m. Display almost always stopped when they landed, unless the nestlings called.

Duration.—High-intensity display was performed in little bursts 5–30 sec long. Several parents whose squawking young I had caught and released displayed continuously for 10–12 min while I stood motionlessly near the young; intensity fluctuated repeatedly between high and medium. A male that had displayed 11 min began to feed a begging fledgling 1 min after I released it; his mate quit displaying after a total of 12 min, waited 10 more min, then began to feed.

If young birds were held in captivity or if I hissed and stood near them after their release, adults renewed displays intermittently for a maximum of 2 hours; the estimated proportion of time spent actually displaying during several 1-hour episodes (the young called occasionally) was 75%.

Frequency, according to stage of reproductive cycle.—Only six females displayed (weakly to moderately) during active building and one during inactive building, compared to hundreds that did not; no male displayed. One female among some 200 that saw me at the nest on a day of laying displayed (moderate); no male did so. Five females and one male displayed weakly to moderately during incubation; a male gave high-intensity display when I hissed; on probably 2000 other nest inspections I was observed but caused no distraction display. Females whose eggs were hatching fluttered slightly in flight from the nest in about 10% of the cases; three continued to flutter the wings after reaching a perch; one male displayed moderately at this stage. During the first 6–7 days of the nestling interval about half the females fluttered when flushed from the nest, a few displaying slightly after landing; male displays were still very rare. However, on day 6 or 7, I usually banded young; if I climbed the nest tree, all females and many males displayed. From day 8 onward displays by both parents became quite frequent and were invariable and intense if nestlings called in fear. Almost all adults displayed as I approached just after young left the nest, the frequency dropping to 5–10% of my approaches 2–5 days after nest leaving (unless fledglings called in alarm). From 6–16 days after nest-leaving few displays (moderate) were observed, and none thereafter. Two moderate displays were seen when I inspected nests from which predators had recently taken nestlings.

Intruders at which displays were directed.—Only five distraction displays were performed toward animals other than man, two toward snakes and probably three toward birds. One female whose nest had just failed displayed toward a Rat Snake on the ground below it; a female whose young were leaving the nest displayed toward a Racer climbing a tree 10 m from her nest; she approached it to within 2 m. A female displayed weakly when a Blue Jay went to and inspected the nest she was building (see p. 416). A male flew at a Field Sparrow perching beside a young warbler 24 hours out of the nest; he followed the sparrow in flight, then landed and displayed at low intensity. A male near nestlings gave a mild display toward a small animal, possibly a bird, in the grass below.

All high-intensity and prolonged displays were elicited by me, but I saw no predator catch or threaten young as I threatened them. Display toward man may suggest that mammalian predators have been important in the Prairie Warbler's evolutionary history (see Ficken and Ficken 1962; compare Armstrong 1956).

Other behavior during displays.—Distraction displays often were interrupted or accompanied by revealing or interesting incidents. Possible redirection activities (Moynihan 1955) were seizing food and suddenly chasing neighbors attracted by the calling. A male interrupted a display by himself and his mate to engage in a sexual chase; he drove his mate to the ground out of my sight (compare Mayfield 1960: 64). Bill-wiping occurred with no eating having preceded it; it appeared irrelevant and may have been a displacement activity. The aggressive component of distraction display (Armstrong 1956) was emphasized by several instances of gaping: a female at a snake, a male at his mate, a female at me. A male displaying on the ground sang two loud group-A songs. A female displaying at me in wet vegetation during a light rain suddenly began bathing movements.

TABLE 92
RELATIONSHIP OF SONG AND MALE'S FOOD-BRINGING DURING DAY-LONG
WATCHES OF 5 NESTS

Male ¹	Date	Day ²	Total songs ³	Songs related to feeding trips		Total feeding trips for day	Feeding trips accompanied by song	
				N	%		N	%
1	6/6	8	545	295	54	76	67	88
4	18/6	4	326	240	74	51	40	78
3	21/6	8	245	230	94	41	30	73
5	17/7	1	160	13	8	10	4	40
10	25/7	7	71	59	83	24	15	63

¹ Numerical designations are those applied to these individuals in Table 66 and Chapter 21.

² The day the first young hatched, hatching day, is day 1, etc.

³ The series of songs at dawn is excluded; see Chapter 8.

⁴ A song was related to a feeding trip if it (a) was sung when a male was seen with food in his bill, or (b) was sung out of my sight but near the nest and as part of a series that ended with or began after delivery of food. The proportion of songs in the last category was small; e.g. 29 of 295 feeding-related songs of male 1 were sung after feeding.

SEXUAL BEHAVIOR

Copulation was not seen during the nestling interval (see Table 26), but once a male fluttered toward a female foraging near the nest, hovered above her, and sang (compare Nice 1926). She continued to forage, and he flew on. Four times females (two carrying food) performed behavior indistinguishable from full-scale solicitation, but never induced copulation. The males were visible to me in three of the cases; all were 1–2 m from the females, were carrying food, and proceeded to the nest with it. Their failure to respond to the females suggests an alternative interpretation to solicitation, but as a preliminary, four other observations (by three males) must be reported.

As the males just referred to approached nests with food, their mates appeared, at least two of them also carrying food. The males immediately crouched and for 2–10 sec elevated the tail and spread and fluttered the wings. The females made no response to the behavior, which looked like female solicitation. These may have been instances of inverted sexual behavior, although the circumstances were not typical (see Morris 1955). Another possibility is that the male actions were submissive, resulting from alarm produced by the sudden approach of another Prairie Warbler (see Marler 1956: 45; Andrew 1961: 322, 347–348; pp. 44–45). Or the males' posturing and wing fluttering may have been associated with begging for food and have been elicited by the sudden appearance of females carrying it. If the last is true the cases would resemble those of brooding females that fluttered while watching mates approach with food (p. 278). And if this speculation is correct, then some or all instances of what appeared to be solicitation by females (preceding paragraph) may have been begging for food.

SONG

As reported in Chapter 8 (see especially Tables 11 and 12), song frequency decreased considerably after eggs hatched. Most males whose songs were counted during full days of the nestling interval sang at least half their songs (excluding songs at dawn) and sometimes a much larger share within about 1 min before

and 1 min after delivering food. Table 92 shows this relationship and also reveals that most feeding trips were preceded and sometimes succeeded by singing. Proportions of songs associated with feeding trips by males 3 and 10 are especially impressive. In all cases fewer songs were sung after than before going to the nest. The possible function of song in integrating parental behavior has been referred to on pages 67-68 and 277.

FOSTERING BY MALES

In view of male feeding of fledglings that were experimentally introduced to their territories (p. 234), it is not surprising that in natural situations at least two males fed nestlings of neighbors. Both males had lost their mates and fed young on adjacent territories whose male owners had disappeared. Each fostering male had lost nestlings to predators earlier in the season. To illustrate: A male had encroached on the territory of a vanished neighbor and was closely following the latter's mate as she gathered food for 5-day-old nestlings. He accompanied her to the nest and watched her from 20 cm away; she brooded and he left. Seven min later he went to the nest; the female rose and he stood on the rim as though feeding. In the next 4 min he brought food twice, the second time carrying away a fecal sac. He fed the nestlings for at least 3 days, but by the time they left the nest he had lost interest (note that late in the season some males lost interest in their own young; see p. 429). I caught one of the young and carried it calling to where the male perched; he approached and watched but exhibited no alarm.

In contrast to the foregoing, three males took over territories whose owners had disappeared but ignored the nestlings of those owners; one ignored fledglings (see p. 310).

CHAPTER 26

DEVELOPMENT OF THE NESTLINGS

MORPHOLOGY

Neossoptiles.—Table 93 presents numbers, lengths, and colors (after drying of amniotic fluid) of neossoptiles of birds no older than 5 hours. Terminology for regions of pterylae is that of Wetherbee (1957: 348–351), for colors, Palmer (1962: chart at 4). The table is based on examination of live nestlings of all ages and also on at least one preserved specimen of each 24-hour age interval from hatching through 264 hours. Quantity of available information for birds of different ages varies. Numbers of neossoptiles on left and right sides of single individuals sometimes varied, apparently randomly; counts of neossoptiles treat each side of a bilaterally paired region as a separate case.

Neossoptiles at hatching: On the coronal region, 2 individuals recorded had unequal numbers of neossoptiles per side (9 and 10, 10 and 11); 2 other individuals had 8 and 8, and 9 and 9. On the occiput 3 of 5 birds recorded had unequal numbers per side (3 and 4 in 2 instances, 4 and 5 in 1 instance); 2 others had 4 on each side. Descriptions in this subsection should be compared with those of Wetherbee (1958); see also Saunders (1956).

Field sketches show mid-dorsal neossoptiles in a single row on the spine; a preserved specimen 24 hours old also has a single row, but on a 76-hour-old specimen neossoptiles are paired on either side of the spine (compare Wetherbee's 1957: 420 diagram of the basic neossoptile pterylaxis of Parulidae). No upper pelvic neossoptiles were detected (compare Wetherbee 1957: 418); on 2 birds, none were found on the lower pelvic region; but on 1 bird were 2 and on 3 there was 1 neossoptile.

One of 4 birds examined on both sides had unequal numbers of scapular neossoptiles per side (5 and 6); 2 had 5 on each side, and 1 had 4 on each side. On the femoral tract 2 birds among 3 examined on both sides had 6 neossoptiles per side; another had unequal numbers (6 and 7).

Rectrices varied in length and on some individuals were still only barely detectable at age 76 hours. More usually on newly hatched young, rectrix 6 (the longest) was about 2 mm, and 5 through 1 were progressively shorter with rectrix 1 barely emerging from the skin. Rectrices of preserved birds are light (perhaps in life a shade of yellow or flesh); other neossoptiles are darker.

Secondary coverts on one living bird were a single row of 6 feathers; another had a row of 3 with a row of 5 posterior to it. Two preserved specimens have secondary coverts arranged in an anterior and a posterior row, with numbers of feathers per wing asymmetrical: one has 1 anterior neossoptile on each wing, a posterior row of 5 on one wing and 4 on the other; the second specimen has rows of 1 and 5 (posterior) on one wing, 3 and 7 on the other. Sites of emergence of these feathers suggest that anterior feathers probably are middle

TABLE 93
NUMBER, LENGTH, COLOR OF NEOSSOPTILES, ACCORDING TO REGION

Region ¹	Cases	Number ² of feathers		Length, mm ³	Color ⁴
		Extremes	Mode		
Coronal	8	8-10	9	6	dark gray
Occipital	10	3-5	7	6	medium gray or dark gray
Mid-dorsal	4	4-6	4, 6	6-7	medium gray
Pelvic					
Upper	5	0	—	—	—
Lower	6	0-2	1	4	medium gray
Scapular	9	4-6	5	8	medium gray
Femoral	9	4-6	6	7	medium gray
Rectrix	6	6 ⁵	6	2-5 ⁵	— ⁵
Secondary coverts ⁵					
Greater	5	4-7	5	4	medium gray
Middle	5	1-3	1	3	medium gray
Crural	8	0 ⁵	0	—	—

¹ Terminology follows Wetherbee (1957: 348-351).

² See page 285. Where regions are bilaterally paired, the count is for only one side of the body.

³ Decimals are rounded to the nearest whole number.

⁴ Terms follow Palmer (1962: 4).

⁵ See text.

secondary coverts, posterior feathers probably greater secondary coverts (see Wetherbee 1957: 382, 383, 418).

A crural tract was noted in the field on one individual (2 neossoptiles) but was not found on four others. Wetherbee (1958: 235) noted crural down on two newly hatched Prairie Warblers. He also detected four abdominal down feathers on these.

Neossoptiles between hatching and nest-leaving: Neossoptiles on certain regions of a 76-hour-old specimen were fewer than any on newly hatched birds, suggesting that some feathers had been lost. On 6- and 7-day-old nestlings, down was still observable on most or all tracts that had borne neossoptiles at hatching; coronals and mid-dorsals were especially noticeable. At nest-leaving, coronal neossoptiles were still quite conspicuous.

Preserved nestlings of various ages show no evidence that neossoptiles grow after hatching, with the possible exception of unusually long (8 mm) neossoptile rectrices on a 9-day-old bird. Wetherbee (1957: 352-353) reviews conflicting reports on the subject of growth after hatching. No changes in color were detected.

Weight.—Methods: Newly hatched birds that had not yet eaten were weighed on an analytical balance accurate to 1 mg, and such weights were rounded to the nearest cg. Other nestlings were weighed on a pan balance accurate to about 0.1 g, and these weights were recorded without rounding.

Table 94 summarizes weights for the first 6 hours of life, for ages 6-24 hours, and for subsequent 24-hour intervals; maximum error after age 24 hours was 8 hours. The table is based only on healthy looking nestlings in nests containing no cowbirds, except that weights of nestlings under 24 hours of age are included even though cowbirds were present. Data from birds caught within 2 hours after

TABLE 94
WEIGHT OF NESTLINGS, ACCORDING TO AGE

Age, hours ¹	N	Weight, g ²			Mean gain	
		Mean	Extremes	SD	g	% ³
Less than 6	10	1.03	0.8–1.4	0.19	—	—
6–24	10	1.49	1.2–1.7	0.19	0.46	45
24–48	14	2.11	1.6–2.6	0.36	0.62	42
48–72	10	2.94	2.7–3.2	0.14	0.83	39
72–96	9	3.61	3.2–3.9	0.28	0.67	23
96–120	14	4.70	4.3–5.6	0.34	1.09	30
120–144	17	5.68	5.2–6.4	0.34	0.97	21
144–168	10	6.13	5.7–6.6	0.27	0.45	8
168–192	6	6.55	6.0–7.2	0.49	0.42	7
192–216	18	6.04	5.7–6.8	0.33	–0.51	–8
216–240	23	6.46	5.8–7.0	0.33	0.42	7
240–264	6	6.33	6.0–6.6	0.24	–0.13	–2

¹ Except for age "less than 6" hours, some ages were subject to maximum error of 8 hours.

² Weights are rounded to the nearest 0.1 g.

³ Mean gain is divided by the last preceding mean weight.

leaving the nest are included. Figure 31 plots points and shows the curve (drawn by inspection) of the data in Table 94. The figure also plots weights of nestlings in nests parasitized by cowbirds and nestlings evidently suffering inanition in nests not parasitized by cowbirds. Individuals in these two categories often died

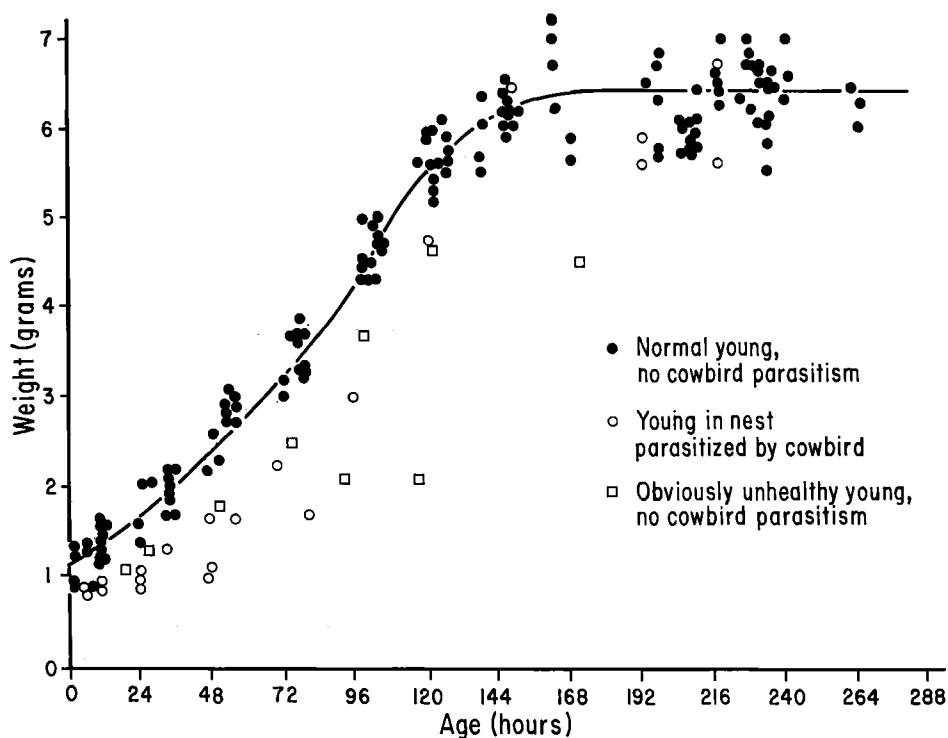


FIGURE 31. Weights of nestlings with and without cowbird nestmates, according to age. Included are weights of individuals caught within 2 hours after leaving the nest. The curve was drawn by inspection, ignoring data from young with cowbird nestmates and young that were obviously unhealthy. See text and Table 94 for details.

TABLE 95
WEIGHTS OF SELECTED NESTLINGS, ACCORDING TO AGE

		Weights, ¹ age in hours						
		3 hours	24 hours	46 hours	70 hours	94 hours	120 hours	149 hours
Nest 1								
Bird A ²		0.8	1.2	1.6	2.3	3.0	4.8	6.5
Bird B ²		0.9	0.9	1.2	dead			
Bird C ³		0.9	1.0	dead				
		10 hours	28 hours	54 hours	78 hours	99 hours	123 hours	193 hours
Nest 2								
Bird D		1.7	2.1	2.9	3.9	5.0	6.1	6.5
		5 hours	24 hours	52 hours	72 hours	99 hours	124 hours	148 hours
Nest 3								
Bird E		0.9	1.6	2.3	3.2	4.5	5.6	6.1
		2 hours	26 hours	52 hours	76 hours	100 hours	124 hours	148 hours
Nest 4								
Bird F		0.9	2.0	3.1	3.8	4.7	5.5	6.2

¹ Weights in g are rounded to the nearest 0.1 g.

² Nestlings hatched no more than 9 hours after a Brown-headed Cowbird nestmate hatched.

³ Nestling hatched 23–29 hours after a Brown-headed Cowbird nestmate hatched.

during the nestling interval (see Chapters 32 and 33). Finally, Table 95 presents weights of five marked nestlings at various ages, three of them from one clutch containing a cowbird nestling.

Weight at hatching: Three nestlings at hatching weighed 0.95 g, 1.06 g, and 1.14 g. One weighed on the pan balance 1 hour after hatching was 1.3 g. The mean of 10 weights taken no more than 6 hours after hatching was about 1.0 g. Walkinshaw (1959) reports hatching weights in Michigan as 1.1–1.4 g. Wetherbee (1961: 417; pers. comm.) and Wetherbee and Wetherbee (1961) weighed two incubator-hatched young from Massachusetts as 0.94 g and 1.00 g.

Unfed newly hatched young weighed slightly less than 75% of the mean weight of newly laid eggs (1.30 g; see Chapter 19). Compare D. K. Wetherbee's statement (in Mayfield 1960: 110) that "most song birds at hatching weigh about 75% as much as their eggs, and wood warblers nearer 70%."

Wetherbee (1961: 428) divided weights of two newly hatched Prairie Warblers by egg volume; the quotient was 0.69. My mean weight for young 1–6 hours old, 1.0 g, divided by my mean for volume, 1.21 (see Table 59), is 0.83.

Based on adult breeding weights (pp. 544–545), newly hatched birds weighed about 13% of mean male weight, 14% of mean female weight. Nice (1943: 72) states that in most passerines neonatal weight is 6–8% of adult female weight.

Changes during nestling interval: The curve (Fig. 31) of weights per day of nest life is sigmoidal, with a slight acceleration of gain during days 5–6 and a rapid leveling off thereafter (compare Hann 1937: 178–179, 228–229; Schrantz 1943: 379–384; Mayfield 1960: 109–110). Mean gain per 24 hours, a percentage of weight at the end of the preceding 24 hours, is shown in Table 94.

The greatest such gains occurred during days 1–3. My small samples suggest that nestlings may have lost weight slightly late in nest life (see below, Pitelka 1940; Eaton 1957: 18–20), when water content and other body constituents probably were changing rapidly (see Ricklefs 1967).

Weight at nest-leaving: Seventeen birds weighed within 1–2 hours of leaving the nest at ages 8–11 days weighed 5.5–7.0 g; the mean was 6.25 g (SD 0.41 g). Based on this mean, fledgling weight was 84% of adult male breeding weight and 81% of adult female breeding weight (pp. 544–545).

Walkinshaw (1959) found in Michigan that three young ready to leave the nest at 8 days weighed 7.6 g, 7.9 g, and 8.7 g, i.e. considerably more than the greatest weight I recorded.

Factors associated with variation at time of nest-leaving: Nestlings in nests parasitized by cowbirds failed to gain weight normally during at least days 1–4 (see Fig. 31 and Table 95). Many died shortly after hatching (see Chapter 32), but some that survived this dangerous time subsequently gained rapidly enough to attain normal weight late in nest life (see bird A, Table 95); other survivors continued to weigh less than average (compare Mayfield 1960: 173–176).

My sample does not show variation in fledgling weight according to age at time of nest-leaving; the three oldest such fledglings weighed were 6.0 g, 6.3 g, and 6.4 g. Statistical evidence that weight varied with brood size is unsatisfactory, but from day 7 onward mean weights from broods of three were some 0.2 g greater than those from broods of four.

Growth of selected external structures.—At ages 0–6, 12–18, and 24–30 hours and thereafter at about 24-hour intervals a few individuals were measured as follows: Gape—inside calipers placed at opposing angles of the rictus; culmen—along total length; tarsus—from heel to the lower edge of the last undivided scute; forearm—from the estimated point of articulation of the elbow to that of the wrist; hand—from the wrist to the tip of the wing, excluding feathers. When nestlings reached age 96 hours, the wing was folded against the body and measured as is the adult wing, with feathers flattened.

Table 96 presents the results. Figure 32 uses means, plotted at midpoint of each 24 hours of age, to show growth curves.

At hatching, the gape was nearer adult size than were any other measured structures. At the end of day 8 it had increased in breadth by 62%. An apparent decrease thereafter may be the result of earlier overestimation; the thickened rictal flange made measurement difficult and somewhat subjective.

The culmen grew steadily during nest life, at nest-leaving was about 200% of its length at hatching, and in full grown birds about 300%. Principal growth of the limbs occurred during days 1–6. The tarsus by day 6 was some 190% longer than at hatching, at nest-leaving was 215% longer, when full grown 230% longer. For the forearm, comparable gains at the same points in life and in the same order were 185%, 215%, and 235%. For the hand comparable figures were 135%, 195%, and 215%.

Mean length (2–6 cases) of the folded wing at various approximate ages was as follows: 96 hours—16 mm; 120 hours—21 mm; 144 hours—25 mm; 168 hours—26 mm; 192 hours—32 mm; 216–240 hours—37 mm.

TABLE 96
MEASUREMENTS OF SELECTED STRUCTURES, ACCORDING TO AGE

Age, hours	Measurements ¹									
	Gape		Culmen		Tarsus		Forearm		Hand	
	N	Mean	N	Mean	N	Mean	N	Mean	N	Mean
0-6	7	6.2	7	3.4	7	5.7	4	4.5	4	5.1
12-18	4	7.0	4	3.4	4	5.6	3	5.2	3	5.7
24-48	2	8.6	2	3.8	2	8.4	2	7.0	2	7.6
48-72	2	9.5	2	4.3	2	10.9	2	9.2	2	9.2
72-96	2	9.3	2	4.6	2	11.8	2	10.0	2	9.3
96-120	4	9.6	4	5.0	4	14.4	2	13.0	2	11.1
120-144	5	9.9	5	6.5	5	16.5	5	14.0	5	11.9
144-168	6	10.2	6	6.1	6	15.9	5	14.0	3	11.4
168-192	4	10.2	4	7.2	4	16.4	2	14.5	—	—
Nest-leaving	3	9.1	3	10.1	3	18.0	2	15.5	2	15.0
Full-grown immature ²	6	8.0	68	13.6	104	18.7	2	16.5	2	16.0

¹ Measurements are in mm.

² Measurements of culmen and tarsus are derived from Table 179 and are intermediate between male and female means.

D. K. Wetherbee (1961: 426, 428, 429), in a study of many species at hatching, reports lengths of various bones of the limbs and pectoral girdle of two young Prairie Warblers and compares these with adult lengths. Hatching lengths were a mean 17% of adult lengths. In most neonatal passerines, lengths of bones averaged only 13-15% of those of adults.

Development of juvenal plumage; colors of unfeathered surfaces.—This section

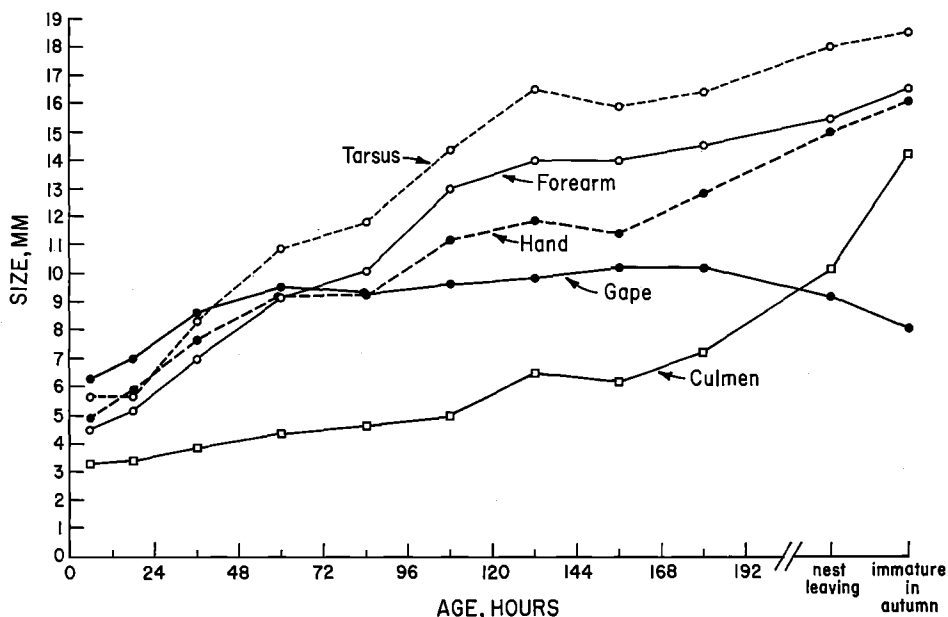


FIGURE 32. Mean width of gape and length of tarsus, hand, forearm, and culmen, according to age of the young. Measurements were at ages 0-6, 12-18, and 24-30 hours and thereafter (prior to nest-leaving) at approximately 24-hour intervals. See Table 96.

is based on field examination and/or photographs of many nestlings whose ages were known to within 8 hours and an inspection of preserved specimens. Table 97 presents lengths of selected feathers at approximately 24-hour increments of age. Selection of certain feathers (e.g. secondary 1) was based on the ease with which development could be followed and different individuals compared. In other cases the identical feathers could not be measured each day on each bird (e.g. a feather of the coronal region), and I selected what looked like representative feathers for the region or tract. The symbol * indicates that no feather sheath projected from the surface of the skin at the age shown. Numbers standing alone or before + refer to length of sheath; numbers after + refer to length of the unfolding feather projecting beyond its sheath. Neossoptiles still adhering to juvenal feathers were ignored.

Terminology follows Palmer (1962: 6-7), but when greater detail was desired I added terms from Van Tyne and Berger (1959: 89-91, Fig. 8-10).

Age 0-24 hours: Teleoptiles visible at hatching were the sheaths of primaries, which could be seen as dark areas far below the skin; sheaths of greater primary coverts and of secondaries 1 and 2 may have been similarly visible. Probably at about 12 hours and certainly at 24 hours dark sheaths of most or all secondaries and of one or more alula feathers were also visible beneath the skin. Hairlike processes projected 0.3 to 0.5 mm from follicles of primaries, their tips curved or hooked, the hooks turned outward toward the tip of the hand. (According to D. K. Wetherbee pers. comm., almost all passerines have these tiny hooked tips on some primaries.) Also by age 24 hours, papillae of the dorsal region (spinal tract) and of the ventral tract, particularly the abdominal region, formed a barely perceptible roughening of the skin on some individuals.

At hatching, body surfaces exclusive of eyes, bill, and feet were colored as follows: the occiput and dorsal surface of the body—very light brownish red; wings—tawny with a slight rufous tinge; ventral surface—about as the dorsal surface, except where the viscera were visible through the nearly transparent yellowish skin (see Wetherbee and Wetherbee 1961); legs and tarsi—tawny with a slight rufous tinge; bill—faintly translucent, buffy yellow at the commissure becoming flesh-colored toward the midline of the mandibles; upper mandible with a faint brownish olive tip; egg tooth toward the proximal end of this colored area. When dorsal surfaces of nestlings aged 4 and 20 hours were compared in the field, the younger birds were more reddish, i.e. darker.

Most of the inside of the mouth was about the same color as the dorsal surface (compare Wetherbee and Wetherbee 1961; Ficken 1965; Skutch 1967: 142, 149, 159, 164). The cartilaginous ridge on either side of the midline of the palate was tinged with yellow, therefore less reddish than the general mouth color. The same is true of that part of the mouth overlain by the tongue.

Age 24-48 hours: Early in this interval rows of papillae became noticeable on the ventral tract of all individuals inspected, producing a roughening of the skin; papillae on regions anterior to the abdomen were darker than the background body color, on the abdominal region were the color of the body itself. The dark papillae of the dorsal region of the spinal tract started to appear. By about 34 hours, scapular and femoral sheaths were visible beneath the skin as rows of dark dots. By about 48 hours, blackish gray sheaths of certain feathers

TABLE 97
LENGTHS¹ OF SELECTED² JUVENAL FEATHERS, ACCORDING TO AGE³ OF NESTLING⁴

Feather	Length in mm ¹ at age ³								
	48 hr	72 hr	96 hr	120 hr	144 hr	168 hr	192 hr	216 hr	252 hr
Primary 4	1.0	3.5	10.0	12.0 + 0.5	14.0 + 3.0	15.0 + 6.0	14.0 + 10.0	9.0 + 18.0	7.0 + 22.5
Greater primary covert	1.0	2.0	5.5	8.0 + 1.0	6.0 + 4.0	no record	1.5 + 13.0	0.0 + 11.0	0.0 + 12.5
Secondary 1	0.5	2.5	7.0	10.0 + 1.0	13.0 + 2.0	14.0 + 6.5	11.0 + 12.0	10.0 + 13.0	6.5 + 20.5
Greater secondary covert	*	2.0	4.0	7.0 + 1.0	6.0 + 4.0	no record	0.0 + 14.0	0.0 + 14.0	0.0 + 16.0
Longest (distal) alula feather	1.0	2.5	4.0	6.0 + 1.0	5.0 + 3.0	5.5 + 4.5	3.0 + 8.0	3.5 + 8.5	0.0 + 12.0
Marginal covert	*	*	1.0	2.0	1.0 + 1.0	no record	0.0 + 2.5	0.0 + 3.5	0.0 + 3.5
Coronal feather	*	*	*	2.0	1.5 + 0.5	no record	0.0 + 4.0	0.0 + 4.0	0.0 + 4.0
Humeral feather	*	1.0	3.0	5.0 + 1.0	3.5 + 3.0	no record	1.0 + 10.0	0.0 + 10.0	0.0 + 11.0
Feather of dorsal region	*	*	2.0	3.5 + 1.0	2.5 + 2.5	5.0 + 5.0	3.0 + 8.0	2.0 + 8.5	1.0 + 11.0
Femoral feather	*	*	2.0	3.0 + 1.0	2.0 + 3.0	no record	2.0 + 8.0	1.5 + 8.5	2.5 + 9.5
Crural feather	*	*	1.0	2.0	1.0 + 1.5	no record	0.0 + 2.5	0.0 + 3.5	0.0 + 3.5
Upper tail covert	*	*	1.0	1.5	1.0 + 1.0	3.0 + 3.0	3.0 + 3.0	3.5 + 4.5	3.5 + 5.5
Rectrix	*	*	0.5	1.0	1.0 + 1.0	no record	5.0 + 1.0	5.0 + 2.0	5.5 + 4.0
Undertail covert	*	*	0.5	no record	1.0 + 1.0	3.0 + 3.0	3.0 + 3.0	4.0 + 4.0	4.0 + 6.0
Feather of ventral cervical region	*	*	*	2.5	2.0 + 2.0	no record	0.0 + 5.0	0.5 + 3.5	0.0 + 5.0
Feather of abdominal region	*	*	2.0	3.0 + 1.5	2.0 + 3.0	no record	2.0 + 6.0	4.0 + 7.0	3.0 + 11.0

¹Lengths in mm are rounded to the nearest 0.5 mm. An * indicates that no sheath had emerged. A single number represents length of sheath projecting beyond the skin. When two numbers are separated by +, the first refers to length of sheath, the second to length of feather protruding from sheath. Neossoptiles attached to feathers were ignored.

²See page 291. Primary 4 is of intermediate length, secondary 1 one of the longest (Table 184). Terms follow Van Tyne and Berger (1959: Figs. 8-10, pp. 89-91).

³Ages were known with a margin of error of 8 hours. Developments prior to age 48 hours are described in the text.

⁴Measurements for ages 144, 192, 216, and 252 hours were made from 1 preserved specimen for each age; other sample sizes were 10.

of the alar tract projected from the skin (see Table 97). A few very small, dark occipital and coronal sheaths were evident beneath the skin, as were dark sheaths of the humeral tract and the entire spinal tract. Crural sheaths, light in color, were visible but not projecting.

The body was somewhat less reddish than on the preceding day. The head was light buffy brown, the pelvic and caudal areas cinnamon, the dorsal and interscapular areas light rufous. Colors of other parts were as at age 24 hours. The tarsi were now tinged with buffy yellow; the bill was unchanged.

Age 48–72 hours: By 72 hours, sheaths of the secondary coverts, the proximal alula feather, and the humeral feathers began to project. Tracts with sheaths not yet emergent or still merely protuberances on the skin (see above) were more prominent than formerly and were widening. Papillae of the femoral tract were visible, as were the upper tail coverts and marginal coverts. The coronal and occipital regions were darkened by many subcutaneous sheaths.

Age 72–96 hours: Sheathed feathers of the marginal coverts, the dorsal region, the femoral and crural tracts, the rectrices and upper and under tail coverts, and the abdominal region emerged. Coronal, occipital, and cervical regions still lacked projecting sheaths. The anal circling was first noted at 100 hours but probably emerged at 72–96 hours. No feathers had yet broken through sheaths. Colors of sheaths were as follows: alar—blackish gray; spinal—sooty black; abdominal—buffy yellow; femoral—anterior sheaths dark proximally and buffy yellow distally, posterior sheaths buffy yellow; crural—many buffy yellow, especially distally, others dark; all other tracts and regions—blackish gray.

Unfeathered surfaces were darker than formerly: back—between light brownish red and chestnut; ventral surface, except where viscera were visible—brownish red; tarsi—flesh underlying a buffy yellow cast on the surface; nails—straw yellow; bill—buffy brown except for the brownish olive tip of the upper mandible; rictal flanges and commissure—buffy yellow.

Field notes made without a color chart describe the inside of the mouth as pink, except for blood red membranes adjoining the corners of the rictal flanges and yellow beneath the tongue.

Age 96–120 hours: On all regions some sheaths were now emergent, many open at the distal ends with feathers projecting about 1 mm. Colors of unfeathered surfaces: dorsal apteria—brownish red; ventral surface anterior to the viscera—brownish red; femur (largely bare)—brownish red; ventral surface of the wing—rufous; tarsi—brownish olive, phalanges with a flesh-colored undertone; bill—brownish olive, except for the olive tip of the upper mandible; rictal flanges and commissure—buffy yellow.

Age 120–144 hours: Some feathers were unfolded on all tracts, and apteria had narrowed considerably. Feather sheaths gave the head a sooty gray color. Elsewhere most sheaths (but not unfolded feathers) were blackish gray to dark gray; however, cream was the color of the abdominal region, the ventral section of the crural tract, the undertail coverts, and the posterior tip of the femoral tract. The rectrices were blackish gray, except that numbers 4–6 were cream ventrally. (Colors of feathers will be described in connection with age 168 hours to nest leaving.)

The tarsi were now harder, hornier, and thinner than formerly, olive with flesh undertones on the phalanges. The nails were turning brownish olive dorsally, were still slightly cream-colored below. The bill color was the same as on the day before.

Age 144–168 hours: See Table 97 for lengths of feathers, which had now unfolded so much that the sheaths on the capital, humeral, femoral, and ventral tracts were visible only when the feathers were parted for examination; without parting, sheaths were readily apparent only around the eye and on the alar tract. Unless the feathers were parted, the ventral apterium showed as a narrow mid-line on the lower breast and abdomen; small areas of skin were apparent on either side of the spinal tract.

Age 168 hours to nest-leaving: The feathers grew and unfolded considerably in this interval (ages 7–10 days) as Table 97 shows, but the appearance of the nestling changed little. Colors of the juvenal plumage at the time of nest-leaving were as follows (compare Brewster 1878): head—dorsally and laterally, dark smoke gray on the frontal, loreal, superciliary, and auricular regions, this color becoming tinged with brownish olive on the coronal and occipital regions; very small cream-colored feathers around the eyes. Wings—primaries dark grayish olive with dark buffy yellow edgings on the narrow vane, the edging becoming smoke gray at the distal end; secondaries the same, except that the distal smoke gray edging continued around the full length of the wide vane; upper primary coverts dark grayish olive, becoming faintly smoke gray distally; upper greater and middle secondary coverts dark grayish olive, the predominantly light flesh edgings on the distal ends producing two wing bars; dorsal marginal coverts brownish olive; ventral side of the hand covered with very short (1 mm) cream-colored coverts. Dorsal body surface—each feather of the spinal tract dark smoke gray proximally, brownish olive distally; the humeral tract brownish olive distally (no information on the proximal segment); the upper tail coverts dark brownish olive. Retrises—dark grayish olive except for whitish spots distally on numbers 5–6 and sometimes on 4. Legs—femoral tract dark gray anteriorly, becoming cream posteriorly; crural tract brownish olive, some feathers edged with buffy yellow. Ventral surface—interramal region unfeathered, the skin brownish red; submalar region dark smoke gray; cervical region brownish olive; axillar region light brownish olive on the margins and distal ends and medium gray proximally and along the raches, resulting in vaguely defined coarse streaks on the breast; abdomen unstreaked, the color between cream and pale gray; undertail coverts the same nondescript creamy pale gray as the abdomen.

Exposed surfaces were colored as follows: tarsi—brownish olive, the phalanges strongly tinged with flesh, nails brownish olive, their tips cream; bill—the upper mandible olive, slightly flesh colored at the base; rami of the lower mandible brownish red, nearly blood (a term not used by Palmer 1962), the rest of the lower mandible brownish red becoming buffy brown 4–5 mm from the tip; the thickened rictal region and commissure buffy yellow. The egg tooth was still present on 2 fledglings 9 days old, but was not detectable on 3 preserved specimens about 10 days old. Notes of field observations made without a color chart report membranes inside the corners of the mouth as blood red, the tongue shaded blood red to pink.

TABLE 98
AGE AT FIRST OBSERVATION OF BEHAVIOR, ACCORDING TO DAY OF
NESTLING INTERVAL

Behavior ¹	Day ²	Behavior ¹	Day ²
Begging	H	Preening	
Turning over	H	Back, scapulars	6
Kicking	H	Breast	7
Calling (hunger calls)	H	Underside of wing	8
Resuming embryonic position	H	Remiges	8
Bracing with wing tips and feet	2	Sleeping with head extended	6
Resting head upright	3	Stretching	
Orienting gape toward sound source	4	Upward-leg-stretch	7
Clutching nest	5	Both-wings-down-stretch	7 (probably)
Surveying surroundings	5	Upward-wing-stretch	8
Flapping and fluttering wings	5	Side-stretch	9
Crawling when on flat surface	5	Jostling	7
Cowering	6	Gaping	8
Squawking	6	Scratching head	9
Jumping from nest, crawling	6	Shaking body	9
Sitting on tarsometatarsi	6	Snapping bill	9
		Perching in nest	9
		Climbing into nest tree	10

¹ Behaviors are described in the text.

² The day the first young hatched is day H; the following day is day 2, etc.

Eyes.—The eyes were closed at hatching, the slit slightly less than 2 mm long. By age 48 hours the slit was 0.5 mm longer. At 72 hours the eyes opened slightly during begging and gaping for food. At 96 hours the slit was 2.7 mm long; the opened eye (top to bottom) measured about 1.5 mm. At 120 hours the slit was 2.8 mm long and the opening, 1.8 mm; at 144 hours the slit was 3.2 mm long and the opening, 2.8 mm. No further measurements were made, but there was little change during the rest of nest life.

BEHAVIOR

This section is based almost entirely on field observations. Some behavior that began shortly after hatching probably went undetected by me for 1–2 days; some descriptions may be incomplete.

Material is organized chronologically. Certain behaviors, especially movements that appeared stereotyped, are listed in Table 98 with ages at first observation. Chapter 9 deals with vocalization of nestlings and Chapter 24 with behavior associated with defecation.

Terms will be defined when used, with the following exceptions: "Begging" is opening the mouth with the head raised, apparently in hunger (see Rand 1941: 217). "Comfort movements" are behaviors used in caring for body surfaces (R. W. Ficken and Ficken 1966: 640–644).

Hatching day.—Turning over: Immediately upon pushing out of the shell, nestlings moved all limbs for 5–10 sec, then lay motionless. When lying on the back and touched, some squirmed and moved the limbs but made no effort to turn over. Others used the head and limbs to right themselves, extending and bending the neck somewhat like an upside-down turtle. Similarly, at age 2 hours some nestlings lay motionless on the back during weighing, but others attempted, some successfully, to turn over.

Moving limbs: Both as a response to tapping on the surface on which they lay and also in the absence of any observed external stimulus, young kicked the feet backward while flexing (clutching with) the digits. When clutching concluded, the hallux was usually in its embryonic position, separated from the other phalanges and stretched back along the tarsometatarsus.

Begging: A nestling that hatched while being watched on a table top raised its head and begged 17 min later, when it was picked up for the first time. Tapping and prodding in the intervening 17 min produced only writhing and kicking. Its initial begging lasted about 1 sec; the head was raised only slightly above the resting position. In the nest, a bird about 18 min old begged when I touched the nest; another less than 30 min old begged both spontaneously and when jarred. No sound by me ever elicited begging by a nestling on hatching day (compare day 2, below). The longest observed duration of begging on hatching day was about 10 sec; the head usually fell forward from its unsteady, nearly upright position after some 3–4 sec.

Resting and sleeping positions: Nestlings usually lay prostrate on the belly with wings and legs somewhat extended; occasionally for at least 1 hour after hatching a bird would resume the essentials of the embryonic position (Chapter 20). Another common posture on hatching day and probably day 2 was lying on the belly with the head slightly to one side, chin down against breast, as though the bird were supporting itself on forehead or crown; this too appeared to be a carry-over from the embryonic position (compare Rand 1941: 217).

Day 2.—Begging: All movements of the preceding day were present but were now more vigorous; e.g. the head was raised higher and held more steadily. The only new behavior observed was thrusting the wings and feet downward for support during raising of the head; this propping was not noted after day 4 or 5 and probably disappeared as nestlings gained strength and began to rest with the head upright against the nest wall (see the next paragraph). Begging sometimes occurred without any observed external stimulus. A brood of four begged immediately after I made a squeaking noise near them.

Day 3.—Resting with head upright: Resting the head, bill pointed upward against the nest wall appeared to replace the prostrate sleeping position of earlier ages. It usually began about at age 72 hours but was seen once in a bird about 48 hours old. After 1–2 min with the head up, nestlings withdrew it and subsided into the bottom of the nest. On very hot days birds with their heads against the nest wall opened the bill for some 30 sec.

Day 4.—Turning over: Nestlings struggled hard to avoid lying on the back (e.g. when I turned them over to sketch the ventral tract); if held with back downward, birds would thrust the head upward and forward, thereby righting the position of the head as much as possible.

Begging: At age about 78 hours, nestlings begged and moved the head to continue to face me as I made squeaking or hissing sounds while changing my position near the nest. The eyes opened slightly during begging, but orientation toward me probably was by audition rather than vision.

Day 5.—Begging: Mouths turned quickly toward a parent arriving with food; young turned toward me and begged when I handled them or jarred the nest. A brood once begged after the male sang and before he was in sight, but this may

have been coincidental since some begging occurred without apparent external stimulation. Words spoken in a normal tone, clicks, and other low sounds from me elicited no response; but high squeaking noises caused begging. Begging young opened their eyes wide and called often.

Reactions to handling; moving limbs; locomotion: Some birds when I grasped them clung to the nest with their feet; one uttered faint cries. Placed on a flat surface nestlings immediately struggled, kicked their feet backward and moved their wings, and progressed forward a few cm; this stopped when they were held in my cupped hand with the head slightly elevated or when they were placed in a container shaped like a nest.

Wing flapping and fluttering: Wing flapping and wing fluttering consisted of synchronous beating of the half-extended and slightly raised wings. Separate terms are used because two variations were observed: Sometimes the wings were raised above the back and beaten in a large arc (wing flapping); at other times wings vibrated or trembled (wing fluttering) with the wrists stretched only slightly to the sides and the primaries extended backward. Flapping gave the impression of exercising or trying the wings; a nestling flapped when climbing to the nest rim (not at this age); possibly the movement assisted progress. Fluttering accompanied begging; Nice (1943: 39) states "[w]ing movement as a releaser of the feeding reactions of the parent is seen in a great many altrices." Wing flapping disappeared soon after young left the nest, as might be expected if the behavior was a precursor of flight or functioned to exercise or strengthen the wings. Wing fluttering persisted until independence. Assuming the foregoing distinction is valid, the two forms of behavior could not always be differentiated. Movements by a bird 110 hours old, the earliest age at which synchronous beating of the wings was seen, could have been of either type but probably were wing fluttering; flapping was not certainly identified until age 168–192 hours.

Surveying surroundings: A nestling that I removed from the nest raised its body and head into the upright position for 5 sec, opened its eyes, turned its head as though able to see, and appeared to survey its surroundings.

Position of brood in nest: Members of the brood often faced in the same direction, heads and bills close together. Sometimes nestlings were in distinct layers, one or two lying on top of the others.

Day 6.—Beginning of fear reactions: I banded most nestlings at this age, and few displayed fear. When not sleeping, those awaiting banding often sat passively upright, tarsometatarsus and heel on the ground, and begged toward me. An occasional nestling evinced strong fear, retracted the neck, and crouched (cowered) in the nest. Several squawked (see Chapter 9) when picked up, and a few jumped out of the nest after being returned to it. If frightened nestlings were prevented from leaving the nest on their first attempt to jump out, they usually went to sleep; but one or two got to the rim 2–3 min after having been returned to the nest, plunged to the ground, struggled forward several cm, and lay still.

Begging: Birds begged at the jolt caused by a parent's landing below the nest and out of their sight, at slight jolts of the nest by me, sometimes (apparently) at the male's song nearby. My touching the body had no effect, but my squeaking continued to cause begging. Nestlings when awake and active

greeted parents noisily, thrusting their trembling heads toward them and almost jumping at them. Begging sometimes continued 30–40 sec after feeding had been completed, even after adults had left the nest. Short bursts of begging also occurred when no parent was present.

Preening: Poking the bill at the body surface and nibbling or working at feather sheaths with the open bill were first noted at this age. The only region toward which the bill appeared directed was the back (and scapulars), but other parts may have been preened too (compare Nice 1943: 16, 43; Mayfield 1960: 108). Small ants once crawled onto a nestling I had placed on the ground; it twitched or shuddered and three times thrust its open bill at an ant on its humeral region; the movement resembled preening (compare Nice 1931: 219).

Social bond within brood: Nestlings evidently were attracted to each other and experienced satisfaction at contact. I once placed a brood of four in a trap in an effort to catch their parents, scattering the nestlings at random on the ground; when I returned all were sprawled on top of each other. I separated them and left but soon returned and found them clustered tightly together; this was repeated several more times with the same result.

Sleeping, resting, dozing; orientation in nest: Beginning on this day and continuing until nest leaving, most birds spent 50–60% of the period 0900–1800 with the head resting on or hanging over the rim of the nest. Older nestlings kept the bill open on the rim much of the time (especially when warm) with the body extended and sprawled; this posture may have cooled them through evaporative water loss, but I once saw a bird with extended head and open bill at a time when air temperature was only 17.2°C. The only other sleeping position noted at this age consisted of lying in the bottom of the nest with head and neck drawn in, bill sometimes pointed upward and sometimes to one side. Before 0800 and after 1900 nestlings usually were immobile and accepted food almost passively; some 75–90% of the periods just after dawn and shortly before darkness appeared to be spent in sleeping or dozing (eyes closed) deep in the nest. Young did not arrange themselves in the nest in any discernible pattern; sometimes all faced in one direction, sometimes all caudal regions almost touched in the center of the nest, etc.

Day 7.—Preening and stretching: Preening of the breast was first observed. Stretching was seen at age 160 hours; the earliest stretch looked like those components of the upward-leg-stretch (see p. 497 and compare Ficken 1962b) that could be performed while lying in the nest; the movement must have involved simultaneous extension of both legs, but this was not visible. The head and shoulders rose slowly above the level of the rim, then sank back after 1–2 sec; the upward thrust was directed slightly forward at times and concluded with a movement suggesting falling forward or bowing. Probably a function was to free the actor momentarily from the weight and confinement caused by its nest mates.

A second, both-wings-down, stretching movement also occasionally seen on this day became frequent in older nestlings: Young high enough in the nest for most of the body to be visible simultaneously thrust the wings downward and slightly backward (see p. 301; see Nice 1943: 44, Ficken 1962b).

Begging, hunger reactions: Begging was occasionally accompanied by wing fluttering (above), and association of these movements soon became almost invariable. Some broods regularly begged noisily, others did so rarely; the behavior was now almost never directed toward me (see next paragraph). Calls (see Chapter 9) probably expressing hunger were occasionally audible from birds deep in the nest (i.e. not begging); captive nestlings gave such calls even when apparently asleep.

Fear reactions: Most nestlings showed fear toward me, uttering Squawk and struggling to escape when picked up. One aged 168 hours jumped from the nest when I picked up its nestmate, but most only crouched or cowered unless touched. Birds that jumped to the ground began to crawl immediately but had difficulty overcoming the obstructions of plants. They soon tired and quit crawling and 15–20 min later were still only 1–2 m from the point of fall.

A form of cryptic behavior beginning at this age was probably an extension of cowering: In order to band broods in high nests, I usually waited until day 9 or 10, climbed the nest tree, with my hand over the cavity removed the nest and put it in a paper bag, and dropped the bag to the ground (sometimes 10 m below). Despite the swaying of the tree, nestlings usually crouched silently in the nest while I climbed; rarely one would Squawk and jump out. More striking, most broods remained in the nest throughout the episode; upon descending I would find the nest upside down in the bag, the young huddled together and clinging to the bottom with their feet. Once I sawed down a large tree to get a nest with a brood of 9-day-olds; they did not leave it even when the tree crashed to the ground.

Jostling: Next to preening, jostling was the most frequent and conspicuous behavior during late nest life, becoming very noticeable on day 7. The actor wriggled and thrust its body upward several times; when finished, it usually was higher in the nest than its nestmates and occasionally had shifted position horizontally. Jostling appeared associated with discomfort and crowding.

Bouts of activity: On this day and increasingly until nest leaving, intervals of simultaneous activity by most or all of the brood were followed by periods of sleeping and dozing. Active periods were characterized by constant preening, jostling, stretching, and very vigorous begging. Periods usually lasted 2–5 min, occasionally 10–12 min, and were about twice as frequent before 1230 as afterward (least frequent at about 1700); they became more numerous and started earlier in the day as nest-leaving approached, and they also involved increasingly diverse behavior. Intervals of dozing and sleeping on day 7 lasted 10–35 min (mode about 15–20 min) and became shorter, at least during the morning, as nest-leaving approached. Arrivals of parents during inactive interludes evoked little begging.

Synchronization of restlessness probably arose from the crowded condition of the nest; any nestling's jostling and changing position doubtless affected the whole brood. Occasional violent tossing and bouncing suggested that a nestling was trying to extricate a foot or wing.

Day 8.—Stretching: Upward-leg-stretches were very frequent whenever birds were awake from 0530 onward. Upward-wing-stretches were seen for the first time (compare Ficken 1962b; see Chapter 40). The wings were unfolded simultaneously and raised, sometimes no higher than the level of the back and some-

times over the back; the wrists were extended little if at all, and movement was of the proximal wing joints only; the head and shoulders tilted forward somewhat. A common sequence of stretches was both-wings-down, upward-leg, upward-wing.

Wing fluttering and wing flapping: Wing fluttering while begging remained common, and wing flapping now seemed clearly to be a different form of behavior.

Gaping: Nestlings occasionally gaped at me when touched; although the behavior looked about like begging, agonistic motivation was implied by cowering prior to being picked up, absence of wing fluttering or calling, and failure to extend the head toward me (as would be expected during begging). Also some nestlings gave a Squawk upon being handled, then gaped. A bird 10 days old twice opened its mouth widely for 1–2 sec toward a nestmate.

Effect of bad weather on behavior: Broods exposed to heavy rain reverted to an earlier stage of behavior, becoming inactive and sitting silently during banding and weighing. I liberated a bird of this age in a tree and made a squeaking sound to attract an adult; the young turned toward me and begged with all usual accompanying movements.

Day 9.—Preening: Preening was now directed at the undersides of wings and remiges; thus nestlings probably preened all parts of the body. Movements looked identical to those of adults (see Chapter 40) but were sometimes slower; they often preceded or followed stretching and once followed a body shake (see below). Sometimes an entire brood preened simultaneously for 10 min. An associate once saw a nestling apparently poking at the side of the nest, behavior regarded by Ficken (1962b) as misdirected preening in young American Redstarts.

Begging: Some broods called regularly in the absence of adults, making enough noise to increase the risk of predation (see Chapter 33).

Wing flapping: Increasingly often, wing beating was independent of begging. A nestling would rise higher than its mates, flap with great energy for 3–4 sec, and subside into inactivity. An individual climbed up the nest wall (but not to the rim), preened for 2 min, flapped vigorously, then slumped back into the nest.

Head scratching: Head scratching (see Chapter 40) was observed. Usually it was impossible to see whether the foot was over the wing (indirect scratching, the method of adult Prairie Warblers) or under it (direct). Twice nestlings appeared to scratch directly (fledglings occasionally did so); certain young parulids scratch directly (Ficken and Ficken 1958).

Body-shaking: Twice nestlings on day 9 engaged in body-shaking (see Chapter 40). In at least one case the plumage was noticeably erected, which evidently is a component of this behavior in various other species (see Ficken 1962b, R. W. Ficken and Ficken 1966: 642). The order of shaking and feather erection was not noted.

Cowering: Entire broods sometimes simultaneously retracted their necks suddenly (compare incubating females, pp. 223–224); in the only case in which the cause was observed, it appeared to be an American Robin flying 2 m overhead. Once a nestling was begging vigorously as the male approached with food; when 10 cm away the male turned aside and retreated; the young vanished immediately into the nest and emerged only when the male returned 90 sec later.

Blue Jays calling nearby evoked no discernible response, nor did Chek or Tsip calls of the female towards me (compare responses to calls at age 10 days, below).

Climbing, perching: Nestlings that I placed on the ground moved not only along the ground but also now climbed upward in the vegetation. Occasionally a bird moved spontaneously from the nest cavity and almost to the rim, appearing to grasp the upper wall with the toes and hold itself upright by resting partly on its nestmates.

Stretching: Side-stretch was performed but details (e.g. foot movements, if any; see Chapter 40) could not be seen. Ficken (1962b) regards both-wings-down as a transition behavior in some species, giving rise to side-stretch and then disappearing. However, in two broods of Prairie Warblers, both side-stretches and both-wings-down-stretches occurred repeatedly during nest-leaving (on day 10); and I saw the latter stretch three times in fledglings 9–13 days old. Further, several adults appeared to extend both wings downward slightly in conjunction with upward-stretches (a sequence common in nestlings), and I conclude tentatively that the side-stretch does not entirely displace both-wings-down in Prairie Warblers. The most frequent stretch on day 9 and for the remainder of the nestling interval was the upward-leg-stretch; both-wings-down was slightly less common, upward-wing-stretch considerably less so, side-stretch least.

The sequence (one stretch immediately following another) most often observed was both-wings-down, upward-leg, sometimes followed by upward-wing. Other comfort movements and activities sometimes preceded or succeeded stretches, among them preening, head scratching, and wing flapping. One young when leaving the nest performed an upward-wing-stretch just before flight.

Behavior on day 10 and thereafter.—Many broods left the nest when the oldest members were about 216 hours old (Chapter 27); in broods that stayed longer, little new behavior appeared. Climbing to the nest rim was seen some 10 times before the day of nest-leaving and usually was followed by preening while the nestling perched unsteadily. In perching, the legs and feet were flexed; the tarsometatarsi and tibiotarsi formed the most acute angle possible, and the belly seemed to rest on the folded leg and foot. At the end of most perching episodes the young fell backward into the nest, but one turned around on its perch and faced the nest to enter it. Climbing to the rim was restricted to the morning hours except for one instance: A bird 230 hours old climbed out of the nest at dusk (1958) and moved upward 25 cm through branches, opening its wings while climbing. Its mother fed it once and it climbed down to the nest; it left again, but climbed back and was on the rim at dark. The female was also on the rim or high in the cavity. The brood left before 0515 next morning (compare the usual hours, Chapter 27).

Nestlings at this age begged when the female called Chek but became silent when she called Tsip (compare p. 316).

CHAPTER 27

DURATION OF THE NESTLING INTERVAL; DEPARTURE FROM THE NEST

THE NESTLING INTERVAL

The "brood nestling interval" began with hatching of the first young and ended with departure of the last young to leave the nest. Total hours between these events were divided by 24, and length of the interval is stated in days, with any remainder treated as a whole day. Thus, if the first egg hatched at 1900 on 1 June and the last nestling left at 0600 on 10 June, the interval is 9 days long. One brood nestling interval at a nest that produced a Prairie Warbler and a cowbird is included in the sample; the cowbird's history is ignored.

The "individual nestling interval" is equivalent to age at nest leaving and is stated in hours, rounded to the nearest hour. When either an individual's hatching or its leaving the nest, or both, took place between nest inspections, individual nestling intervals are subject to error; margins of error were calculated and are presented as described in Chapter 23. Intervals with margins of error exceeding 8 hours were eliminated from the sample. As a result, many broods provided only one or two individual nestling intervals. Margins of error were ignored in calculating mean and standard deviation; the mean margin was 5.1 hours.

Data were rejected from nests (1) whose young were restless and difficult to restore after banding, or (2) at which experiments were performed, or (3) that were too high to permit inspection. Since many broods left the nest late in the season (p. 398), when mean nest height was greatest (Chapter 15), the last limitation severely reduced sample size.

The word "fledge" is not used because of its ambiguity, but a bird that had left the nest permanently is a "fledgling."

Brood nestling interval.—Of 38 brood nestling intervals, 4 were 8 days long, 17 were 9 days, 15 were 10 days, and 2 were 11 days. The mean is 9.4 days (SD 0.8 days).

The decision to include 8-day intervals requires explanation, because leaving the nest probably was premature. One brood left because the birds' growing weight tipped the nest and spilled them out; a heavy storm probably contributed. Another brood apparently left because of irritation by ants. Reasons for departure by two other broods are unknown. None of the young in the four cases could fly, and they were clearly ill-prepared for life out of the nest; one that I examined after the severe storm was cold and lacked vitality. The smallest fledgling from the ant-infested nest was on the ground and near death; I never saw it again, but its siblings survived. The cases are included in the sample because accidents, irritation from insects, etc., are probably recurrent and must affect significant numbers of broods. Excluding the 8-day cases, the mean brood nestling interval for 34 broods would be 9.6 days (SD 0.6 days).

Walkinshaw (1959) reports 3 brood nestling intervals from Michigan, 1 of 10 days and 2 of 8 days. Daniel (1901) states that young remain in the nest about

TABLE 99
AGE OF NESTLINGS AT TIME OF LEAVING THE NEST

Age, hours ^{1, 2}	N
191-200	9
201-210	9
211-220	32
221-230	8
231-240	20
241-250	10
251-260	3
261-270	3
Total	94
Mean ³	224.1
SD ³	17.5

¹ See page 302 for the methods used.

² The mean margin of error is 5.1 hours.

³ Margins of error were disregarded.

10 days in Virginia. Jay M. Sheppard sent me very useful notes regarding a nest in Ohio; the brood nestling interval was 10 days.

Individual nestling interval.—Table 99 shows ages, grouped by 10-hour unit intervals, at which 94 nestlings left the nest. Minima were exactly 192 hours (both hatching and leaving were observed) and 192 hours (m.e. 8 hours); the maximum was 264 hours (m.e. 8 hours); the mean was 224.1 hours (SD 17.5 hours). Distribution of intervals was bimodal; arranging the data by hours, not by 24-hour unit intervals, the modes fall at 214-221 hours (34 cases, 36%) and 234-242 hours (24 cases, 26%). This clustering around 9 days and 10 days probably was produced in part by the tendency of eggs to hatch during daylight (see p. 239) and of young to leave the nest in the morning (see below).

Margins of error at 10 nests were less than 30 min; 5 additional nests had margins of 1 hour. The shortest of these precisely defined intervals was about 192 hours, the longest about 241 hours. Between the extremes, times of the other cases were distributed about as in Table 99.

Factors possibly associated with variation.—Table 100 distributes brood nestling intervals according to brood size when nest leaving began; intervals of 8 days are omitted because nestlings probably left for reasons irrelevant to brood size. The table suggests that small broods remained longer in the nest, which is con-

TABLE 100
LENGTH OF BROOD NESTLING INTERVAL,¹ ACCORDING TO SIZE OF BROOD
AT NEST-LEAVING

Length, days ²	Brood size at nest-leaving				
	1	2	3	4	5
9	0	3	5	7	1
10	1	4	6	4	0
11	0	0	2	0	0
Mean length according to brood size	10.0	9.6	9.8	9.4	9.0

¹ The brood nestling interval began when the first young hatched and ended when the last young left the nest.

² Intervals of 8 days are omitted; see pages 302, 303.

TABLE 101
 HOUR AT WHICH YOUNG LEFT THE NEST¹

Hour	Number of young		Cumulative % out of nest
	Out of nest ²	Still in nest	
0600	3	69	4
0700	13	65	17
0800	35	58	38
0900	54	34	61
1000	58	19	75
1100	78	13	86
1200	95	11	90
1300	95	7	93
1400	103	4	96
1500	103	4	96
1600	110	0	100
2000 ²	129	0	100

¹ Methods are described in the text, this page.

² At 1700, 1800, 1900, and 2000 no young were still in the nest; numbers of those that had left fall between 110 and 129.

sistent with observations of what appeared to be discomfort associated with crowding from day 7 onward (Chapter 26; compare Schrantz 1943: 384; see Nice 1943: 18–19, Davis 1955: 289–290).

In view of the foregoing, suggestive evidence that the brood nestling interval became longer as the season progressed and as—during part of the season—brood size decreased (see Chapter 33) is not unexpected; of 9 broods that left prior to 11 June, 6 had 9-day intervals and 3 had 10-day intervals. Between 11 June and 30 June (inclusive) 3 broods had intervals of 9 days, 4 of 10 days, and 1 of 11 days. After 30 June, 8 intervals were of 9 days, 7 of 10 days, and 1 of 11 days. Variation by date independent of brood size is not apparent.

HOUR OF NEST-LEAVING

Some nest-leaving was directly observed, but most young left nests between my frequent inspections at this stage. Cases in which departure was not observed fall into two groups: (1) At an inspection at nightfall the young were in the nest, and by early next morning they had left; or (2) young left between two inspections on the same day. In order to use the various kinds of data available, I have tabulated for each hour of the day of nest-leaving absolute and relative numbers of young already out of the nest and numbers still left in it. The following illustrates this method in the various kinds of cases: If I saw a nestling leave at 0829, I tabulated it as in the nest at hours prior to and including 0800 and as out at 0900 and subsequent hours. If I knew that a bird had left on a certain day sometime before my first inspection, e.g. an inspection at 1036, I tabulated it as out of the nest at 1100 and subsequently; I made no entry for the hours 0600–1000. If I found a bird in the nest at 0926 and out at 1215, I tabulated it as present from 0600 to 0900, absent from 1300 to 2000; for 1000–1200 I made no entry. The frequency and timing of my inspections at the time of nest-leaving probably produced a fairly accurate estimate of the distribution of times of nest-leaving.

Table 101 requires no comment. Extreme hours of nest-leaving were as follows: Two young left a nest by 0515 on a rainy morning (see p. 301) and two left another between 1530 and 1830.

At four nests I made systematic continuous observations until all young left (13 nestlings), which they did between 0645 and 0914. Departure of some members of five additional broods was observed by chance, also within the times just stated.

Jay M. Sheppard (pers. comm.) saw the first nestling from an Ohio brood of four leave at 0450 EST; the last left at 0615.

THE NEST-LEAVING INTERVAL

The interval between times at which the first and last nestlings of a brood left is the "nest-leaving interval."

At the four nests watched continuously, nest-leaving intervals were 22 min, 23 min, 52 min, and 104 min. Exact times of departure by individuals, with semicolons separating one brood from another, were 0852, 0907, 0910, 0914; 0752, 0753, 0815; 0722, 0741, 0814; 0645, 0654, 0829. An Ohio brood of four watched by Jay M. Sheppard (pers. comm.) had a nest-leaving interval of 85 min.

Turning to departures between inspections, six intervals separating inspections at six nests were 165, 175, 240, 240, 270, and 300 min; these are, of course, maximum nest-leaving intervals. Similarly, if it is assumed that no nestling left before 0515 (see Table 101 for the justification), then the time elapsed between 0515 and the hour of an inspection at which the nest was found empty establishes the following outer limits for 21 additional intervals: 15 min—1 case; 30 min—2; 90 min—6; 150 min—2; 210 min—1; 270 min—5; 330 min—4.

In 58 of 60 cases all broodmates left on the same day; twice leaving was prolonged over 2 days. Young began to leave one of the latter nests when the oldest were 8 days old and the youngest was 7. The 8-day-olds were a few cm from the nest at 1545; the youngest (about 175 hours old) was on the rim, where it remained for the rest of the day and at least late into the night. In the other exceptional case, two of a brood of three left between 1030 and 1200; at 0845 next day the third young was still on the nest rim. All of this brood were at least 216 hours old when nest-leaving began.

It is likely that the first nestling to leave did so because of some combination of factors that includes degree of development and comfort in the nest. This first departure, or possibly the fledgling's loud calling (see below) after leaving, probably affected young still in the nest but now less crowded and became an added and strong stimulus to their nest-leaving. For the final nestling, isolation may have been yet another stimulus to leave (see p. 307). Nothing suggested that behavior of adults contributed to departure of either the first or last nestling to leave; e.g. food was not withheld.

Nest-leaving intervals probably rarely were more than about 2 hours long. Recalling that many hatching intervals were much longer (Chapter 23), ages of broodmates often differed considerably when they left the nest (see Hann 1937: 186, Schrantz 1943: 384–385, Mayfield 1960: 110–113). Hatching and nest-leaving intervals of the 10 broods for which I obtained both data are shown below;

no young died during the nestling interval in these nests. Hatching interval is given first preceding the dash, and semicolons separate the intervals of different broods: about 25 hours—22 min; 5 hours—52 min; 11 hours—2 hours; 16 hours—1 hour 44 min; 12 hours—23 min; 12 hours—about 15 min; 17 hours—4 hours 30 min or less; 13 hours—2 hours 4 min or less; 20 hours—about 20 hours; 22 hours—about 16 hours. The last two cases are those in which nest-leaving was prolonged over different days.

These data and many others less precise imply that it is advantageous to evacuate the nest quickly once a broodmate has left. Presumably, average gains outweigh average losses imposed by leaving at a time determined not so much by the individual's own condition and motivations as by those of its siblings. The advantage gained is probably the reduced risk of predation. Almost invariably the first fledgling called noisily, as described below. Any predators attracted to search the vicinity would doubtless find the nest more readily than they would individual fledglings, which were much smaller and less conspicuous than nests; and the danger of remaining in the nest seems clear. The heavy nest predation on the study area (Chapter 33) is sufficient indication that predators could be expected to investigate any nest they spied. Evidence that predators are in fact attracted by activity associated with nest-leaving follows: I sometimes took young ready to leave the nest and put them in one cell of a multi-celled trap as bait to lure their parents. A chipmunk (a predator on birds—see p. 415) entered one trap, a Racer another; the snake entered the cell with the fledgling and ate it, but the chipmunk was unable to do so. On or beside other traps and looking in at fledglings were a Broad-winged Hawk, a Racer, and an undetermined rodent.

BEHAVIOR ASSOCIATED WITH NEST-LEAVING

Adult females.—Numerous casual and several systematic observations indicate that very rapid feeding (one trip/3–4 min) was usual in the final hours of nest life; but one female, a relatively infrequent feeder during the nestling interval, fed only three times between 0545 and 0829 on the day young left. Three of four females whose broods were observed throughout nest-leaving distributed food about equally among fledglings and young still in the nest; one fed only fledglings. Once a female unsuccessfully proffered an insect to a sated young on the nest rim; after 1 min she turned to the empty nest and made thrusting, food-offering movements toward the cavity for 30 sec; disposition of the food was not seen.

Nest sanitation continued as long as any nestling remained. A female whose brood had already left a nest that was badly infested with the mite *Ornithonyssus sylviarum* spent 3–4 min delousing the nest (or satisfying hunger?).

The growing uneasiness or restlessness of some females during the last days of the nestling interval reached a new height on the day of nest-leaving. Some called Chek (probably not at me) every few seconds while foraging.

A female was at her high nest when the first nestling flew from it; calling loud Cheks she trailed 0.3 m behind until the fledgling landed (compare page 280).

Adult males.—In the continuously observed cases of nest-leaving, males fed much less than females just prior to departure (one male had disappeared). A

male brought no food while the female made 17 trips; another made 6 trips to the female's 44; still another made 1 trip to the female's 18. Once a male offered food at a nest that all young had already left (compare Nice and Nice 1932).

Males seemed not to share females' generalized excitement or alarm just before nest-leaving. A male tending a motherless brood (p. 261) was at the nest when the first nestling flew from it; he followed right behind it, like the female described above.

Comfort movements of nestlings.—Young performed comfort movements frequently and persistently both just before leaving the nest and afterward; bouts of preening and stretching often lasted 1–2 min. All stretches were seen, side-stretches becoming more frequent (or more easily observed) after birds were out of the nest cavity; during side-stretches some young lost their balance and spread the wings to regain it.

Other nestling behavior.—Occasionally birds that had been drowsy awoke and left the nest with few preliminaries. To illustrate: The sole nestling remaining in a nest evidently slept for 38 min, awoke and called like a fledgling for a moment, suddenly jumped to the rim, and immediately made an unusually long flight.

Nestlings on the rim and in the nest tree often slept 1–6 min, until adults arrived with food. When asleep they pulled the head down between the shoulders, pointed the bill upward at 45°, flexed the tarsi and appeared to rest partly on the belly; the body was rather erect, its axis pointing upward at about 60° (as in the Kirtland's Warbler fledglings in Mayfield 1960: frontispiece; see also frontispiece, this work).

Climbing to the rim and occasionally even a few cm into the nest tree, rare before the day of nest-leaving, was frequent for 1–2 hours preceding departure. Wing flapping often assisted in getting to the rim and for a few hours after nest-leaving was common during perching. Birds at times moved around the rim before reentering the nest, then usually faced the cavity and jumped in (compare p. 301). During interludes on the rim and on twigs, nestlings sometimes perched with feet and legs extended, as adults perch. Intervals out of the nest ranged from 5–10 sec to 1–2 min.

The tail bobbing characteristic of adults (p. 501) was seen in two nestlings, once just before taking off in flight from the nest and once while apparently trying to maintain balance on the rim.

Pecking at a small insect was observed for the first time in a nestling 10 days old and perched on the rim. The bird seemed to watch an insect, then reached down at it but failed to catch it (compare Mayfield 1960: 109).

Fledglings almost always began bursts of loud, frequent (typically about 45 calls per 30 sec), vibrant calls (p. 78) as soon as they were away from the nest. Some 24 hours later the calling had become rare unless adults failed to bring food as often as it was wanted. Loud calling just after nest-leaving probably functioned to maintain contact during dispersal and possibly to reorient parental attention away from the nest. Nice (1930a: 345) believed "the act of leaving the nest had set in motion the food calling instinct" of Black-throated Blue Warblers. However, I sometimes heard the last nestling in the nest calling indistinguishably from its dispersed siblings, and I suggest that in the Prairie Warbler the new state of isolation from nestmates is associated with the change in vocal behavior.

Nestlings' manner of leaving nest.—Some nestlings climbed and hopped into the nest tree, occasionally accompanying hops by wing movements and usually stopping several minutes between each move. When 10–40 cm from the nest, sometimes as much as 20 min after leaving it, they flew. Other nestlings flew (one plunged to the ground) immediately upon climbing to the rim. An occasional bird on the point of flying tried at the last moment to check itself, clinging to the nest and tipping over forward. Longest flights were made by the oldest broods watched. First flights covered 0.5–10 m; the mode was 2–3 m. A second flight of 2–5 m usually followed within several minutes. When tossed 3 m straight up into the air to test their ability to fly, most birds just out of the nest flew at least 5–6 m; some could make no forward progress and managed merely to break the fall by beating their wings. Half those that flew could maintain a level course or even gain height; the rest lost altitude steadily and landed. One bird leaving the nest made a 180° turn while covering 7 m in flight; the rest flew straight.

Occasional fledglings seemed unable to alight on a perch and descended to the ground, but most that could fly headed straight at a tree or shrub and hung there flapping and teetering. Occasionally young called loudly during the first flight.

CHAPTER 28

THE INTERVAL BETWEEN LEAVING THE NEST AND INDEPENDENCE

DURATION

All post-embryonic life prior to separation from parents is the "period of dependence." The pair bond often dissolved when young left the nest; the adults drifted apart, each caring for particular fledglings. Groups made up of at least one parent and one offspring are "family units." Their composition rarely changed in the period of dependence except as young disappeared. Most independent young soon left the study area, which poses the usual problem of distinguishing between disappearances resulting from death and from departure. The difficulty is especially great when disappearance was at an age close to the normal age for attaining independence (below). As a standard for evaluating such cases I have used data from family units consisting of more than one young in which all young disappeared simultaneously and the adult remained. Many such simultaneous disappearances occurred between ages 40 and 50 days, suggesting a rough mean and a normal maximum length of the period of dependence and implying an approximate minimum of about 35 days. Behavior of fledglings is consistent with the view that 33–35 days is about the earliest age at which they could survive unassisted; one individual that left its parents at age 35 days is known to have survived. I have used 34 days as the minimum period of dependence and treat fledglings disappearing earlier than that (the adult member of the unit remaining on the home range) as having died.

Length of the period of dependence is stated for family units instead of individuals, because siblings in the same unit cannot be assumed to have behaved independently. However, sometimes unit members did disappear on different days (extreme, 5 days apart). In such cases I have measured that period to the departure of the last young seen with its parent, since birds that disappeared shortly before that may have been overlooked.

Disappearance of the entire family unit, including the parent, normally meant that it had wandered off its home range and sometimes the study area. Some units moved considerable distances, usually when the young were almost self-sufficient, and in cases in which all members disappeared simultaneously after age 33 days dependence may have continued for some unknown interval. Arbitrarily, I have included in the sample such cases of disappearance (six) in which the young were at least 35 days old and have treated dependence as lasting 1 additional day after my last sighting of the unit.

Extreme periods of dependence were 34 and 55 days long; the mean for 50 family units was 40.8 days (SD 3.6 days; see Table 102). Periods did not vary according to sex of attending parent or date (compare Mayfield 1960: 120–121, Hofslund 1959: 169).

Given the difficulty of establishing that observations of feeding fell on the final day of the parent-young association, details tending to prove that some

TABLE 102
DURATION OF PERIOD OF DEPENDENCE, ACCORDING TO SEX OF PARENT
LEADING FAMILY UNIT¹

Period, days	Cases according to sex of parent		Total cases
	Male	Female	
34	0	1	1
35	1	2	3
36	3	3	6
37	3	2	5
38	3	2	5
39	1	0	1
40	4	1	5
41	3	2	5
42	1	3	4
43	1	1	2
44	3	1	4
46	1	4	5
48	1	0	1
50	0	1	1
53	0	1	1
55	1	0	1
Total	26	24	50
Mean	40.6 days	41.0 days	40.8 days
SD	4.4 days	5.1 days	4.6 days

¹ The period of dependence began at hatching and ended when the adult delivered food for the last time, inclusive of both days. Methods are described on page 309. The family unit consists of the parent and the young under its care; see page 309.

periods lasted only 34 and 35 days are of special interest. (1) A female brought off a brood after her mate had disappeared. A new male occupied the territory and courted the female as she cared for her fledglings. During long observations by me the male never fostered the young. When the brood was 33 days old (i.e. on its 34th day of life) the female quit feeding and began a second-brood nest. The young disappeared. (2) A pair brought off five young. When the survivors were 35 days old, the parents ceased to respond to begging and the female began a second-brood nest. The young disappeared; one was seen when 74 days old.

Effect of attempts to produce a second brood; polygyny.—Attempted production of a second brood appeared to shorten the period of dependence of some first broods, as just noted, but not all. Four males behaved as follows when second-brood eggs hatched: Two probably quit feeding their fledglings, which were 38 and 40 days old, respectively; 2 fed the nestlings but also tended the first brood, one until the fledglings were 55 days old, one until they were 47 days old.

Polygynous males sometimes confronted a situation like that above. In three instances, periods of dependence of the older brood were 37, 37, and 40 days. When eggs of the younger brood hatched, one of these males fed only the nestlings; two fed both broods (see pp. 267, 368). The male that fed only nestlings almost surely caused the period of dependence of his older brood to be abbreviated; the fledglings remained on the territory for 3 or 4 days untended, uttering hunger calls and sometimes begging. Once the male flew at and supplanted a fledgling that was following him and calling (compare Stewart 1953).

Responsibility for terminating the period of dependence.—As just noted, parents sometimes put an end to dependence, but I believe that the young terminated

most relationships. Instances in which members of the same unit became independent on different days suggest this, since a parent would be unlikely to ignore one young and continue to feed another. Further, aggressive acts toward fledglings were rare, whereas I saw countless feedings of young fully capable of caring for themselves. Finally, late in the period young often moved away from the family unit and foraged alone for a time (see below), suggesting a weakening of the bond with the parent.

Occasional associations probably ended accidentally because young became separated from the unit. I sometimes found isolated birds 35–40 days old 300–400 m from the parental home range, uttering loud hunger calls and begging from passing Prairie Warblers.

MORPHOLOGICAL DEVELOPMENT AFTER NEST-LEAVING

Disappearance of neossoptiles.—Neossoptiles were not noted on the back of fledglings after age 10 days. Those on the crown occasionally persisted at least until age 17 days.

Growth of tail and wings.—At age 15 days the tail appeared 15–25 mm long and by age 20 days was 31–38 mm long (8–15 mm short of full length). The tail of a 23-day-old measured 41 mm, and within 2–4 days of that age rectrices were full length.

Changes in length of remiges could not be easily detected in the field. Mean wing length at nest-leaving was about 37 mm; the wings of the 23-day-old specimen were 52 mm, about adult size (see Chapter 41).

Postjuvenile molt.—Traditional terminology is used, with that of Humphrey and Parkes (1959) in parentheses when a molt or plumage is first referred to. Terms for feather tracts and regions follow Palmer (1962: 6–7), supplemented by Van Tyne and Berger (1959: 89–91, Figs. 8–10). Information is drawn from observations of free-living and netted young and from 4 collected specimens aged 23, 34, 43, and about 48 days.

Postjuvenile feather replacement was partial, conforming to Humphrey and Parkes' (1959: 19–20, Fig. 4c) "variation number 3." Rectrices, remiges, upper greater primary coverts, and feathers of the alula were not replaced (compare Stewart 1952, Mayfield 1960: 143, Foster 1967b: 171).

Condition of postjuvenile-molt on specimens of known age.—Age 23 days (sex unknown): Capital tract—many sheaths of the first nonnuptial plumage present on the frontal, auricular, and loreal regions; few sheaths on the coronal, postauricular, and occipital regions. Spinal tract—many sheaths 4–5 mm long on all regions, some with feather ends projecting about 1 mm; all concealed by juvenal feathers. Humeral tract—many sheaths, some with feathers emerging about 5 mm. Femoral tract—many sheaths 3–4 mm long, feather ends projecting 1–2 mm. Alar tract—many sheaths of the dorsal and ventral marginal coverts present, feathers projecting 1–2 mm; sheaths of probably all under greater and middle primary coverts present, the ends just emerging on the proximal sheaths; sheaths of probably all under greater and middle secondary coverts present, feather ends 1–3 mm long; folded wing 52 mm long, hence primaries probably full grown. Caudal tract—tail 41 mm (compare Nolan and Mumford 1965); rectrices sheathed about 7

mm at the base; sheaths of anal circlet present, feather ends just emerging. Ventral tract—many sheaths on interramal and submalar regions; few sheaths on the malar region; many sheaths on the cervical region, some with feather ends just emerging; many sheaths, some with feather ends about 6 mm long, on axillar and sternal regions; many sheaths 2–3 mm long on the abdominal region, concealed by juvenal plumage. Crural tract—many sheaths, most with feathers projecting 1–2 mm. Rictal bristles—absent on specimens at the age of nest leaving, present and approximately full length at this age.

Age 34 days (female): Capital tract—frontal, superciliary, occipital, and coronal feathers full length, many sheathed at least half their length; loreal molt complete; many conspicuous sheaths on ocular, auricular, postauricular, and temporal regions, some with feather ends projecting 3 mm. Spinal tract—heavy molt on all regions, superficially concealed by unfolded ends of some feathers of full length but sheathed at the base; some feathers still short and entirely sheathed. Humeral and femoral tracts—same stage as spinal tract. Alar tract—remiges full length; upper middle primary coverts, apparently 2 in number, almost full length but half and entirely sheathed, respectively; sheaths of upper greater secondary coverts 7–9 mm long, with feather ends just emerging; sheaths of upper middle secondary coverts 3–4 mm long, with feather ends 1 mm long; few marginal coverts still sheathed at the base; molt complete on all underwing coverts. Caudal tract—condition of upper tail coverts not clear: some juvenal feathers present and no incoming sheaths found; rectrices full length, undertail coverts irregularly developed, some half length but sheathed at the base and others only 5 mm long and sheathed; anal circlet sheathed at the base. Ventral tract—a few interramal feathers still sheathed at the base; nearly all feathers of submalar, malar, and cervical regions full length but more or less sheathed at the base; feathers of sternal and axillar regions unevenly developed, with many short and entirely sheathed, many full length but sheathed at the base, and some fully developed; abdominal region with many juvenal feathers largely concealing emerging ends of incoming first nonnuptial feathers. Crural tract—molt complete.

Age 43 days (female): Molt complete except as indicated. Capital tract—many feathers sheathed at the base on coronal, occipital, auricular, postauricular, temporal, and superciliary regions. Spinal tract—a few feathers on interscapular and pelvic regions sheathed at the base. Humeral and femoral tracts—traces of sheaths at the base of some feathers. Caudal tract—both upper and undertail coverts full length, sheathed about 5 mm at the base. Ventral tract—sheaths at the base of a few submalar, cervical, sternal, and axillar feathers and many abdominal feathers.

Age about 48 days (male): Molt complete except as indicated. A few feathers on the cervical and dorsal regions of the spinal tract still sheathed at the base; upper tail coverts about 13 mm long, half sheathed. A few feathers on the posterior part of the abdominal region sheathed at the base; one undertail covert fully sheathed. Some auricular feathers still sheathed at the base.

Duration of postjuvinal molt.—In light of the foregoing, it seems probable that the individual completes postjuvinal molt at the age of about 60 days. If molt starts at age about 20 days (see Table 103), the full process lasts about 40 days. Mayfield (1960: 143) reports that young Kirtland's Warblers begin postjuvinal molt

TABLE 103
AGE AT STAGES OF POSTJUVENAL MOLT

Feather tracts and regions ¹	Development of first nonnuptial plumage	Age, ² days	
		Earliest case	Approximate mean ³
Ventral			
Submalar	Sheaths became visible	27	28
	Molt ceased to be visible	32	33
Cervical	Sheaths became visible	23	26
	Feather ends unfolded, merging with sternal feathers in an inverted V	26	28
Sternal-axillar	Molt ceased to be visible	29	31
	Sheaths became visible	22	24
	Feather ends unfolded forming bars on sides of breast	25	27
	Juvenal plumage still visible in center of lower breast	27	31
Abdominal	Molt ceased to be visible	29	35
	Molt ceased to be visible	33	37
Alar			
Marginal coverts	Became visible at wrist	23	24
Upper greater and middle coverts	Sheaths became visible	31	33
	Molt ceased to be visible	38	39
Capital			
Frontal	Sheaths became visible	22	24
	Molt ceased to be visible	29	31
Coronal	Sheaths became visible	25	27
	Molt ceased to be visible	31	33
Occipital	Sheaths became visible	26	27
	Molt ceased to be visible	30	34
Temporal-auricular	Sheaths became visible	28	30
	Molt ceased to be visible	36	40
Superciliary-ocular	Sheaths or feathers became visible	30	33
	Molt ceased to be visible	35	37
Spinal			
Cervical	Sheaths or feathers became visible	27	28
	Molt ceased to be visible	38	40

¹ Data were obtained from free-living banded young; see text. Tracts are arranged about in the order in which molt became evident.

² A bird is treated as 1 day old on the day after it hatched.

³ Sample sizes were 10–20 individuals. Means are approximate.

at age about 26 days and that it is “essentially complete” at age about 43 days, but he would probably regard the Prairie Warbler’s molt as equally complete at about this latter age. Foster (1967b: 175, 196) reports a molt duration of about 2 months in Orange-crowned Warblers.

Appearance of free-living birds in postjuvenal molt.—Table 103 presents approximate earliest and mean (N = 10–20 individuals) ages at which certain stages of progress became visible. Members of a brood at times differed by 2 or 3 days in attaining a given stage of molt.

To summarize progress of visible molt: Yellow (no color chart used) non-nuptial feathers first appeared in a short narrow bar on each side of the upper

breast adjacent to the wrist of the folded wing. Nearly simultaneously yellow began to show on the wrist itself and very soon afterward on the throat, where it met the yellow bars of the breast and joined these to form an inverted yellow V down the sides. The arms of this V continued to extend posteriorly and their width increased; within a few days the unfolding yellow feathers covered the entire breast; the abdomen remained covered by juvenal plumage. Meanwhile sheaths appeared on the forehead, then on the crown and nape; as feather ends emerged and masked further progress of the molt on these regions (except for some messiness), the sides of the head began to show many sheaths. At about the time at which the appearance of the head became somewhat neater (new feather ends started to conceal the molt somewhat), replacement of upper wing coverts except greater primary coverts began; their sheaths were conspicuous. The final portion of the juvenal plumage to disappear was around the vent, anterior to the new yellow undertail coverts. The last traces of messiness or sparseness in the new plumage were on the nape (made noticeable by head movements) and sides of the head.

Weight.—Mean weight and greatest weight at nest-leaving (Table 94 and Fig. 31) were slightly lower than most weights of fledglings. Two fledglings collected at age 23 days and 34 days each weighed 7.8 g. A female at age 43 days weighed 6.8 g, another at age about 45 days 7.3 g. A male at about 48 days weighed 8.0 g. Since the nonnuptial plumage weighed 0.6 g and 0.5 g in two instances (Nolan and Mumford 1965), weight gain after nest-leaving seems only partly attributable to increased weight of plumage. Berger found that captive Kirtland's Warblers attained their "maximum" weight at about age 20 days (Mayfield 1960: 122).

Bill, tarsi, eyes.—The bill reached full length by about age 14 days, but the thickened rictal flanges were detectable until about 25 days. In a 23-day-old fledgling these structures were 3.2 mm long, approximately half their size when the same bird left the nest. The bill of a 26-day-old examined closely through binoculars was indistinguishable from the adult bill. The color of the rictal flange of a 23-day-old was buffy yellow (Palmer 1962: chart at 4); the color of the rest of the bill was as in adults.

BEHAVIOR OF FLEDGLINGS, ACCORDING TO AGE

The period of dependence is divided into segments 5 days long, the first ending with the 15th day of life counting hatching day, i.e. at age 14 days. Stereotyped behavior, e.g. comfort movements, that seemed to be identical to adult behavior is referred to here but described in Chapter 40. Table 104 summarizes ages at which various behaviors were first observed. Vocalizations are described in Chapter 9.

Age 9–14 days.—Perching: Fledglings recently out of the nest perched at least 95% of the time, usually in shaded and concealed spots in the interior of dense clumps of trees, in clusters of vine-covered branches, or in centers of rounded shrubs and trees. In trees with a vertical trunk, they often perched within a few centimeters of the trunk. Extreme perch heights were 0.3 and 3.0 m, the mean of 99 records 1.43 m (SD 0.74 m). The perching position was usually the one described on page 301; an adult-like position (feet and legs extended) was

TABLE 104
AGE OF FLEDGLING AT FIRST OBSERVATION OF VARIOUS BEHAVIORS

Behavior	Age, days ¹	Behavior	Age, days ¹
Pecking (and eating?) objects	10	Pecking attacker (probably ⁷)	25
Shuffling wings ²	10	Scanning undersides of leaves	
Wiping bill	11	for food	26
Sleeping with bill on shoulder	13	Preparing caterpillars	
Hovering to take food from plant	18 (probably ³)	by beating	28
Congregating with		Flycatching	28
broodmates	about 20	Manipulating nest material	29
Flicking tail after defecating	20	Chasing ⁴ broodmates	33
Gaping ⁴	23	Supplanting ⁴ broodmates	40
Sunbathing	23	Performing tense crouch ⁴	40
Hanging upside down to feed	24	Performing flutter-up ⁴	41
Leaving family unit ⁵		Accepting food in tip of bill	40
to forage	about 25	Assuming position resembling	
Bathing in dew	25 (probably ⁶)	female solicitation ⁸	46

¹ A bird is treated as 1 day old on the day after it hatched.

² See text, this page, and page 496.

³ See page 317.

⁴ Agonistic behavior is described in Chapter 7.

⁵ A family unit consists of the parent and the young under its care.

⁶ See page 319.

⁷ See page 319.

⁸ See page 320.

assumed occasionally, especially shortly before and after most changes of location and also during stretching and head scratching.

Locomotion: Flight was preceded by a momentary tensing of muscles, extending the legs and feet, and bobbing the tail. A 40-m flight was performed by an 11-day-old 24 hours out of the nest. Another 11-day-old whose flying powers I tested by repeatedly approaching it flew 25 m, gaining altitude; it then landed but immediately flew 20 m; after 3–4 min it flew 30 m, performing a 90° turn; 10 min later it was fatigued and flew 20 m but could not maintain altitude; it landed on the ground and was easily caught. By age 12–13 days, birds flew strongly for at least 50 m, and I could not catch them; they could turn only gradually and usually flew a straight course. Despite their abilities, unless disturbed they flew infrequently (0–2 time per hour) and rarely farther than 15 m. Occasionally a fledgling flew toward a parent after being fed; the stimulus for most flights was not detected.

Hopping (sometimes assisted by wingbeats) and sidling one foot at a time along branches were frequent. Birds often moved a few cm in one direction and immediately returned to the original location; sometimes they turned to face in the opposite direction. Tail bobbing was frequent before or after moves; occasionally birds lost balance and recovered it by beating or extending the wings. Early proficiency in hopping is illustrated by the case of a 9-day-old still unable to fly. When placed in an upright glass tube 3 cm in diameter and 10 cm deep, it jumped straight upward to the top of the tube and perched there.

Behavior while perched: Much time was spent in comfort movements, especially preening; some bouts lasted 4–5 min. A bird 10 days old performed a bathing movement called “wing shuffling” by Ficken (1962b; see p. 496). The fledgling when wet with rain preened, stretched, then for 30 sec repeatedly shuffled the wings in bursts of rapid movement; at the conclusion (after 2 min) it erected or fluffed its feathers and left them erect for 1 min.

Bill wiping was first observed at age 11 days. It did not differ from adult behavior, including the characteristic alternate wiping of each side and opening the mouth just before and during wiping.

All stretches that had been performed by nestlings continued. The complete both-wings-down-stretch was last seen at ages 12 and 13 days, each time combined with and probably slightly preceding the upward-leg-stretch. The latter sometimes concluded with the caudal region higher than the head, with the bird leaning forward. In the upward-wing-stretch the head and neck were thrust forward very noticeably; stretching of one wing and then the other probably was noted once. During an aggregate 3 hours' observation of 5 fledglings, I counted 27 upward-leg-stretches, 20 side-stretches, and 9 upward-wing-stretches. Series of stretches were common, with no detected tendency for particular combinations to occur. Preening (including all adult behaviors) often preceded or followed stretches or other comfort movements.

Head scratching was frequent and was indirect except for two observations of direct scratching, at ages 9 and 14 days; in the latter, a fledgling appeared to scratch its left side directly and immediately thereafter its right side indirectly. The foot stretched slightly backward before being lifted over the wing. Body shaking was common, often after preening.

Sleeping, dozing, resting, eating: Fledglings usually dozed or slept about 50% of the time during my long observations; the head and neck were retracted, the bill pointed forward and upward 45° from horizontal. Eyes were closed from a few sec to 4–5 min; the body of very young birds often rocked slightly; rocking stopped by age 14 days. A 13-day-old closed its eyes, placed its bill on the scapular region without tucking it into the feathers, and maintained this position for 30 sec (compare Nice 1943: 58, Eaton 1958: 227, Ficken 1962b). Between intervals of dozing and sleeping, young birds surveyed their immediate surroundings, often appearing to stare intently at nearby leaves and twigs. Sometimes the objects of their attention were insects; rarely, from age 10 days onward, a fledgling would reach out toward an object and apparently eat it. Birds probably could see for a considerable distance; they seemed to detect and watch me when I was 10–15 m away.

Vocal behavior, responses to adult vocalizations: In exceptional cases birds called for 20–30 min without stopping on the first 1 or 2 days after leaving the nest, but usually they gave only occasional short bursts of calls, apparently in hunger. Intensity of calling correlated closely with intensity of begging behavior when fed. Many feedings took place in silence and unaccompanied by begging; very hungry birds called shrilly and continuously while receiving food. After long inattention from a parent, fledglings often called (Harsh Cheks) upon hearing the male sing. A bird aged 10 days that I removed from its parents for several hours called whenever any Prairie Warbler sang, even if the version differed from its father's preferred version (see Chapter 8). Calling after songs and, in older birds, flying in the singer's direction continued throughout dependence.

Tsip calls by adults caused most young to remain motionless and silent for 30–45 min when I was nearby, after which they resumed calling despite Tsip calls; presumably hunger and habituation were responsible. Tsip calls became increasingly infrequent as young grew older and were rare by age 25–30 days,

perhaps because flight superseded cryptic behavior as the most important self-protective behavior.

Other behavior: When air temperature was about 27°C, fledglings sometimes perched with the bill open for several seconds. The bill was also opened during apparent yawning.

Begging like that of nestlings (Chapter 26) continued at this age and throughout dependence. The feet and legs were in the folded position, and the fledgling was therefore somewhat crouched; wing fluttering was frequent, the head and neck trembling and the rest of the body vibrating slightly. Hungry birds occasionally held the bill open while the adult was near and sometimes followed the adult briefly.

I could approach most birds to within 1–3 m if I moved slowly and had not frightened them previously. Usually they called Squawk when they flew (to a high perch above my reach).

Age 15–19 days.—The only new behavior observed was hovering (below); the period was characterized by increased movement and by greater skill and assurance in performing behaviors acquired earlier. Fledglings often perched in the adult position, dozed less, and flew more readily—faster, farther, and less often in a straight line. The Harsh Chek hunger note became less common and less vibrant, Seep and Chek more frequent; young called more when changing location than when motionless. Hungry birds moved toward the adult more often but still perched and waited for food about 90% of the time. Heights and types of perches were unchanged. Young associated with each other very rarely but occasionally toward the end of the interval two or three followed a parent simultaneously.

Foraging: Frequency of pecking at nearby objects increased greatly. Insects were captured but probably not often; apparent testing of the edibility of fruits, twigs, spots on leaves, etc. was common. Thus, an 18-day-old repeatedly took a green grape in the tip of its bill and seemed to squeeze it. Sometimes birds touched leaves with the bill and might have been drinking dew or rain. An 18-day-old appeared to hover at a plant as if removing an insect; the next observed case of feeding by hovering was at age 29 days.

Roosting: At 2014, 34 min before civil twilight, an 18-day-old tended by a male flew into a clump of trees at a height of 0.6 m, immediately fell silent, and disappeared for the night.

Age 20–24 days.—The most conspicuous development was the onset of gregariousness. Periods (20–30 min) of infantile behavior, i.e. inactivity and begging while perched, alternated with periods when behavior was almost like that of adults. By age 24 days flight appeared fully proficient, but before flying fledglings still sometimes crouched uncertainly or made false starts suggesting reluctance. Preening and other comfort movements were common; dozing was rare; and perching birds scanned their surroundings, watched and caught insects, and picked at spots on leaves and twigs. Few indications of fear of me remained; I could sit 10 m from a fledgling for 15–20 min and watch it and take notes.

Gregariousness; agonistic behavior: Members of some family units were still dispersed (10–50 m apart); but most now associated closely for 30

min or more at a time, then separated and perched quietly alone. Birds sometimes were only 10 m apart. To illustrate, three fledglings were never more than 15 m apart during 1 hour; if one flew to a branch on which another was perched, the latter sometimes permitted close approach, sometimes sidled or hopped away. Agonistic behavior began; e.g. when a 23-day-old moved toward another 10 cm away, the latter gaped. When perched together, young often performed comfort movements. At times the unit followed a parent about, usually calling loud, frequent, slightly vibrant Harsh Cheks; Seep calls became more frequent when gregariousness began (see pp. 77, 79).

Foraging, perching, feeding: Active foraging was common, but probably 80–90% of food was still received from parents; e.g. I saw a young (begging, fluttering) take 10–12 meals in succession from an adult and make no effort to catch its own food. Following and begging alternated with waiting; waiting birds rarely called except when the adult approached.

Records of perching heights show no significant change from heights at earlier ages, but birds 20–24 days old occasionally flew up to branches 9–10 m high, usually when following an adult.

A fledgling 24 days old hung upside down, *Parus* fashion, to take an insect from a leaf (see p. 490).

Comfort movements: Two behaviors observed for the first time were lateral tail flicking, a side-to-side movement of the cloacal region after defecation (at age 20 days), and sunbathing (at age 23 days).

Age 25–29 days.—Members of family units probably spent over 50% of the day together, but still occasionally perched alone in sheltered or covered spots. Adults still seemed to provide most food; young followed them noisily and waited passively about equal shares of the time. The infantile mode of perching, uncertainty prior to flying, and dozing nearly disappeared.

Individuals began to leave the family unit to forage alone for several min, flying 30–40 m directly away from the adult; e.g. a 29-day-old did this 3–4 times per hour, after each excursion returning to about the same spot, where the adult fed it. Other evidence that fledglings of this age tended to return again and again to certain sites is presented on page 324. With increasing following of the parent and more active foraging, young birds moved higher into trees, but they still spent a large proportion of time at or under 3–4 m. They also spent less time in dense growth, now sometimes moved through sparsely covered fields and low open scrub, and were easier to find.

Foraging and feeding: Pecking at inedible plant parts continued. New foraging and feeding behavior consisted of examining undersides of leaves (age 26 days), preparing caterpillars by beating them on a branch (age 28 days), and flycatching (age 28 days). A fledgling caught an insect on the wing, dropped it, then twisted and turned in the air in a very skillful and successful recovery of it.

Behavior toward siblings: Apparent begging was once directed toward a sibling 10 cm away by a bird 25 days old (compare Hann 1937: 193). The fledgling to which the movements were directed reached over and touched the now-closed bill of the bird that had begged; both then opened their bills (gaped?). A few minutes later, one of the two flew to a perch just above the other, and reached down to it as though feeding it. I was not certain whether food was passed.

Behavior toward man: Behavior often seen in independent young was noticed for the first time: A fledgling approached me to within 3–4 m and watched as though curious; sometimes such young called Chek and bobbed the tail as though nervous, but often they simply perched and watched. When I hissed, fledglings approached immediately.

Roosting: Two family units (two young each) came together at dusk and foraged directly toward a sumac thicket which they often frequented during the day. Judging by their behavior and final disappearances, they probably went to roost at a height of about 1 m near each other and the male parent; the time was 2010 (35 min before civil twilight). However, one fledgling and the female then left this thicket and roosted close together in a Flowering Dogwood 100 m distant. (Next evening the family did not use these same roosts.)

Other behavior: Preening and stretching became less frequent, possibly as flight and other locomotion increased. The earliest instance of dew bathing probably occurred in a bird 25 days old, but the behavior was too brief to be sure; the next observation of dew bathing was in a bird aged 49 days. A 29-day-old landed on an Osage Orange limb from which loose ends of bark fiber projected; it seized these with the bill and tried (unsuccessfully) to pull them off, using motions exactly like those of a female gathering nest material (p. 141). (In the only other observation of building behavior, an independent immature 55 days old pulled off large shreds of fiber from a dead elm, held them for several seconds, then dropped them; this was repeated 12 times in 2 min.) A 2-day-old attacked by an adult White-eyed Vireo leaned far backward and fluttered its wings above its back, appeared to peck at the vireo, then flew away.

Age 30–34 days.—Noisy gregariousness continued, alternated with short intervals of foraging alone. The family unit now spent more time following the parent and rarely waited passively to be fed. The infantile perching posture disappeared; but at times fledglings approached by a food-carrying adult crouched, causing the body and head to be lower than the head of the parent (see Mayfield 1960: 119). Adults often seemed as attentive to young of this age as to 10-day-olds, and for long periods each day probably more than 50% of a fledgling's food was delivered by its parent. Billing and pecking of vegetable matter became infrequent. A 34-day-old saw a woodlouse (isopod, Oniscoidea) on the bare ground, and flew down and pecked at it several times, attempting to eat it or testing it like a piece of vegetation. A common mode of adult feeding, viz. very rapid seizing of clustered tiny objects such as aphids, was noted in a bird at age 31 days. A 33-day-old flew at a sibling in a brief chase, the earliest such case.

The mean of 82 recorded perching heights was 3.9 m (SD 3.1 m); in a *t*-test comparing this mean and that for fledglings less than 15 days old (p. 314), $P < 0.001$.

Age 35–39 days.—No new behavior was observed. Although some or all young could now survive independently, one carefully studied 35-day-old brood caught little more than 50% of its own food and continued to spend half its time following a parent and begging. Fledglings still sometimes perched 4–5 min and called hungrily. The only other traces of juvenile behavior were occasional billing of plant structures and continued gregariousness. Close association with siblings (with some agonistic gaping and chasing) was still the rule, but solitary foraging

increased. Fledglings showed considerable interest in calls of younger Prairie Warblers; e.g. a 35-day-old flew up to me when a fledgling I was carrying called, and a 43-day-old approached calling nestlings and examined them.

Age 40 days and thereafter.—Feeding, foraging: Beginning at age 40 days young sometimes took food from the parents by seizing it in the tip of the bill rather than receiving it in the wide-open mouth. Occasionally caterpillars taken in this way were held for several seconds before being swallowed.

Behavior toward other Prairie Warblers: A 40-day-old begged and fluttered its wings toward a sibling, eliciting no response. I observed two brief episodes resembling adult sexual behavior. (1) Two siblings age 46 days (on the parental home range but possibly newly independent) were a few cm apart; one crouched and raised its tail nearly vertically in a position resembling female solicitation; neither vibration nor wing movement was noted. The other did not respond and after 2 sec they parted. (2) A 54-day-old had left its father's territory 1–2 hours earlier in the day, after a long period of dependence. It approached a dependent 41-day-old, which crouched briefly in the tail-cocked female solicitation pose; no wing movement or vibration was seen. One of the two (I thought the older) extended and fanned its wings and seemed to walk toward the other, as in male sexual behavior (see Chapter 10).

From age 40 days onward, chases and gaping were often seen in brief encounters with adult and immature Prairie Warblers and small birds of other species. Newly observed agonistic behavior was supplanting (of a sibling by a 40-day-old); flutter-up (by a 41-day-old approached by a female American Goldfinch); and tense crouch and gape (by a 40-day-old toward a brood mate 3 cm distant).

Roosting: A brood of three 40-day-olds begged noisily and moved toward a thicket to which they often went. At 1955, 50 min before civil twilight, they flew into the thicket at a height of 1–2 m and instantly fell silent. The attending male sang occasionally until 2001.

ALLOCATION OF FLEDGLINGS BETWEEN MEMBERS OF PAIR

Stability of family unit.—Only once did a family (two adults and two young) fail to separate into units shortly after nest-leaving. Usually a bond between a particular parent and certain fledglings appeared to form quickly, probably sometime within 1–2 hours of nest-leaving. The best evidence of the degree of stability of these units comes from cases in which both male and female remained on the territory and attempted no second brood. In this situation the young had maximum opportunity to change from one adult's unit to the other; but in eight broods observed throughout the period of dependence, no permanent change was observed. In two of the eight I never saw one parent give food to an offspring belonging to the other's group. To illustrate: I was watching a 35-day-old member of the male's group when its mother and 2 begging siblings passed 5–10 m away, the female feeding her charges. The male's fledgling had received no food from, and probably had not seen, its father for 5–10 min; but it paid no overt attention to the other unit nor they to it (compare Mayfield 1960: 115). In the other six broods, one adult, usually the male, fed the other's charges occasionally. For example, the two parents' units would be somewhat separated on a particular day;

more or less intermingled 1–2 days later, with one adult occasionally feeding a ward of the other; and separated again next day with their original memberships intact.

In every case in which a female attempted a second brood the male took over care of all dependent young and the units merged no later than the laying of the second-brood eggs. With one probable exception (pp. 267–268), females that had begun to incubate did not respond to fledglings. Even when the second-brood nest failed and care of the first brood could have been resumed, four females disappeared either immediately or within 1–2 days of the failure; two others left the male's territory briefly after the failure but returned and nested again. However, a female that built two fragmentary second-brood nests (see Chapter 12) cared for fledglings after abandoning the first fragment; upon quitting work on the second she disappeared.

Rarely broods of exactly the same age were raised simultaneously on adjacent territories. Young at times intermingled temporarily, but none ever joined an adult not its parent.

Size of family units; possible limit of adult's attentive capability.—Although 4 was a common brood size, no unassisted parent brought 4 young to independence; and considerable evidence suggests that 3 was the most one adult could raise. Once a male and once a female, each having lost its mate, brought 4 young off the nest but raised only 3 to independence; the missing fledglings disappeared sometime before ages 28 days and 33 days, respectively. Five pairs produced 4 first-brood fledglings, and the females made second-brood attempts; 4 of the males had only 3 fledglings left late in the period of dependence, and the fifth male had only 2. In contrast, 2 males raised all fledglings from broods of 3 while their mates incubated second broods, and one female whose mate disappeared raised all young from a brood of 3.

A relationship between first-brood clutch size and the attempt to produce a second brood is suggested by the foregoing data. One of many factors affecting clutch size would seem to be the balance of advantages between (1) laying a large clutch that requires prolonged care of fledglings by both adults if all fledglings are to have maximum opportunity to reach independence, and (2) producing a smaller clutch which the male can attend adequately, thus freeing the female to reproduce again. If only these two factors were involved, any limitations tending to abbreviate the breeding season would be likely to affect the strategy chosen, by reducing the availability of the second option. Thus, the shorter breeding season at northern latitudes may favor laying larger clutches there, as occurs in some species and possibly the Prairie Warbler (see Chapter 18). In southern Indiana, the two possible strategies are not entirely mutually exclusive: a female whose first nest succeeds can tend fledglings until they are independent and still have time to attempt a second brood; at least one female did this. The virtual limitation (one exception) of five-egg sets to first nests supports this argument.

Size of family unit, according to sex of parent.—Only one brood of five left the nest, and I was unable to learn how the young were allocated between parents. With broods of 4, each parent cared for 2 fledglings in 4 cases; the female cared for 3 young and the male for 1 in another; in still another the female had 1 fledgling, and the male's number is unknown (some may have died).

Among 9 broods of 3 fledglings, the parents divided them (unless or until a second brood was attempted) in 8 cases. Of these 8, in 6 the female cared for 2 fledglings and the male cared for 1; in the other 2 the allocation was the opposite. As for the brood of 3 that was not divided, the female left the territory when these were 12 days old and the young went with her (see p. 325). In 6 additional cases broods of 3 were probably divided, but I knew the size of only 1 unit per family. In 3 of these the male had 1 young; in 2 the female had 1 young; in 1 the female had 2 young.

Among broods of two, on three occasions the parents divided the young. In four additional cases, I knew the size of only one unit, viz. one fledgling. As mentioned, one pair with a brood of two did not divide it, and the whole family stayed together.

When brood size was one, once both adults cared for the offspring. Three broods of one I saw fed only by the female, two only by the male; the parent that did not feed probably left the home range in these instances.

Considering only those families among the foregoing in which there were 2 units of known size, the total number of male charges was 19, of female charges, 24.

BEHAVIOR OF ADULTS

Attention to fledglings.—Age 9–19 days: During about 480 min of observation (11 occasions, all times of day, data for sexes similar and pooled), 95 meals were delivered, approximately 1 per 5 min. Variation was great; e.g. a fledgling received 13 meals in 22 min in midmorning while another (not its brood mate) received 4 meals in 60 min at the same time of day. As implied by this, feedings were irregular; doubtless they were affected by the number of young to be fed. A male with 2 fledglings fed one 3 times in 5 min, disappeared for 13 min, fed it again twice in 2 min, disappeared for 8 min, and fed it again 4 times in 4 min. During the male's disappearances he was probably tending the other fledgling.

Adults usually foraged within a few meters of the fledgling being tended at the moment. Almost invariably they delivered one item per feeding, bringing it as soon as caught instead of accumulating food. Items often appeared smaller than during the nestling interval, foraging very rapid and possibly less selective; fledglings were judged to receive more imagoes and fewer caterpillars than did nestlings.

Occasionally during bouts of feeding, for no apparent reason an adult would go without food to the young. For 4–5 days after nest-leaving, parents continued to fly protectively behind fledglings when the latter flew, trailing close (1 m or less) and at times performing distraction display after alighting. Trailing flights (see p. 280) became infrequent after about age 14–15 days; the last was seen when a fledgling was 18 days old (but see p. 323).

Age 20–24 days: Because young were now gregarious, all or nearly all of an adult's feeding efforts could be observed. During about 250 min of watching, about 110 meals were delivered, or 1 per 2.3 min; frequency per fledgling was still about 1 per 5 min. Males tending the entire family while females incubated second-brood nests were extremely active, carrying food about once per min for 15–20 min, then usually leaving the vicinity of the young and taking a 4–5 min recess. Adults with only one ward sometimes delivered

about one meal per min (for 15 min). However, these data and data to follow on frequency of feeding are probably biased toward high rates; during bouts of feeding fledglings were especially noisy and attracted my attention.

Adults still at times prepared food as they had done for nestlings and after softening and delivering it sometimes took it back when it was not swallowed immediately (see Chapter 25).

Age 25–34 days: Feeding rates appeared unchanged; in one observation (2 fledglings) of 130 min I counted 105 feedings, or 1 per fledgling per 2.4 min. An adult tending only 1 young fed it 7 or 8 times in 5–8 min, followed by intermissions of 5–6 min. Parents tending 2 or 3 young took fewer and shorter (1–2 min) rests, appeared to forage nearer fledglings, and seemed in rapid motion for periods up to 1 hour. As at earlier ages, 1 bird was fed 3 or 4 times in succession; attention then switched to another because it flew up and begged.

Age 34–39 days: Young probably foraged for themselves more often, but sometimes adults were feverishly busy, making three or four food deliveries per minute. I saw many items caught within 1–2 m of fledglings.

Age 40 days and thereafter: The number of feedings was distinctly reduced. To illustrate, a female ignored a 45-day-old and ate about 10 insects herself; then she suddenly made 2 or 3 quick food deliveries to the fledgling, lost interest in it for a time, then fed it once. Next day she appeared to supplant it when it begged.

Vocal and sexual behavior.—Vocalizations are discussed in Chapters 8 and 9. Sexual behavior was seen only as a preliminary to the raising of second broods.

Territorial and other agonistic behavior.—Males were less aggressive in defending territory. When caring for fledglings, they often ignored vocalizations uttered within their boundaries if the encroacher was not close by; a trespasser that was visible was usually chased and attacked. Trespassing males that were themselves tending young occasionally were tolerated.

Parents were rarely aggressive toward their own fledglings. Cases of supplanting have been referred to (pp. 310, 323). Twice males flew rapidly at their fledglings (38 and 39 days old) and chased them briefly. Once a male suddenly flew after a flying 29-day-old, overtook it, and seemed to drive it to the ground.

Other behavior.—A female tending a 30-day-old suddenly froze (p. 227) for 1 min when a Broad-winged Hawk was overhead.

Once a male display may have induced 23-day-old fledglings to follow the male. Switching from behavior suggesting nervousness to distraction display (probably toward me) and then to apparent butterfly flight (see Chapter 7) he flew into a thicket. Calling loudly, a fledgling then flew toward the thicket into which the male had disappeared; the other fledgling immediately did the same. Note that female flight-to-male is often preceded by the male's butterfly flight (Chapter 10).

MOVEMENTS OF YOUNG; HOME RANGE OF FAMILY UNITS

Dispersal and movement before age 25 days.—Direction of first flights was apparently random. About 2 hours after leaving the nest, young were scattered around it within approximately 30 m, and by day's end their mean distance from

the nest was 30–35 m. Segregation of family units was not noticeable until 1–2 days after nest-leaving, when fledglings of one unit usually were closer to each other than to siblings of the other unit.

Young produced on territories with open and low vegetation, e.g. blackberry patches and few thickets of trees, moved toward woods edge or overgrown fence rows and therefore were often to be found near territory boundaries (see Chapter 29).

Before young reached age about 25 days I found them an average 45 m from the point at which I had seen them about 24 hours earlier. Maximum change of location in 1 day was 110 m, minimum 12 m. Sometimes movement from day to day continued approximately in a single direction, and a unit gradually left the nesting home range farther and farther behind. Much more frequently, movements cancelled each other out, and the unit remained within the old home range (see below).

Birds whose parents were involved in the building of a second-brood nest tended to stay near the nest.

Change of location from day to day after age 25 days.—From about age 25 days and increasingly thereafter, family units sometimes travelled far and fast. A typical example is a move of 100 m that took 10 min; occasionally units that I followed for 10 min covered 250 m. Now that young could move about freely, the degree of site attachment to the home range of some or all unit members (see below) probably was the factor that controlled the unit's location. The greatest distances between locations of a family unit on successive days (the fledglings were 34 and 35 days old) were 400 m and 500 m.

Formation of preferences for specific thickets after age 25 days.—After long movements became common, a family unit might be met at different times at widely separated places on the same day; and it now became apparent that some had a preferred thicket or clump of vegetation to which they often returned. It seemed that the fledglings were attached to this spot; they would move toward it ahead of the adult or when the adult was not with them.

Manner of progress after age 25 days.—Family units composed of more than one fledgling often moved along in series of flights of 10–20 m, each flight separated from the next by an interval during which the young perched or foraged together while the adult moved about more widely gathering food. One fledgling would then suddenly fly perhaps 15 m to the tree in which the parent was foraging; other fledgling(s) would quickly follow, and there the unit would stay briefly until the next move. This kind of change of location frequently was the result of the tendency of adults to feed only the nearest fledgling. A neglected bird at a distance from the parent would move to it, and any others would follow. Thus the patience or impatience of a bird that had been ignored often determined the pace of the unit's progress, while the general direction of movement (therefore the extent to which it left the home range) probably depended on the parent; see also the following section.

When there was only one fledgling it tended to follow the adult. Whether such units moved more or less often than larger ones is unknown, but some covered considerable distances (e.g. 500 m in 5 hours).

Fidelity to nesting home range (units headed by males).—I observed 55 different male-led family units when the young were at least 20 days old, on a total of about 250 days. Approximately 80% of all sightings were on the male's territory; some 50 sightings off the territory were a mean 100–125 m distant. The maximum distance separating a unit from the territory was 500 m, and 6 other units had traveled 300–450 m. Nineteen of 26 units observed frequently during the period of dependence were never more than 150 m off the territory, and seven were never off it.

In the seven cases (above) in which units made considerable moves, all young were 34 days old or older. I usually found these units on or near the territory until the day they were discovered at a distance; their movement away appears to have been a quick one. Only one unit returned to the territory later. Six of these 7 broods hatched in mid-June or later (3 of them after 13 July), whereas 6 of the 7 broods that I never saw off the territory were produced in first nests whose eggs hatched in May. Thus most long movements of male-led units took place when nearly all males had passed out of breeding condition (Chapter 34); such moves probably were associated with a general decline of territoriality.

Fidelity to nesting home range (units headed by females).—I observed 51 females tending fledglings at least 20 days old, on about 200 days. Approximately 60% of all sightings were on the territory of the female's mate; about 75 observations of units off the territory were at a mean distance of 200–225 m. Of 24 female-led units observed throughout dependence, 16 were never seen more than 150 m from the territory, and 12 of these were never off the territory. The maximum distance a unit had travelled was about 600 m; two other units moved 500 m and 400 m, and several moved 300 m.

Unlike units led by males, those of females often began to move when fledglings were quite young. A unit that ultimately wandered 350 m moved off the territory 2 days after nest-leaving, and 8 others moved away within 7 days of nest-leaving; one of these covered 325 m by the time the young were 14 days old. Some of the females heading these units had been deserted by mates (see p. 429), but others simply left males behind; no such units ever returned to the territory.

Movements of female-led units were not associated with a late hatching date; and of 12 units observed only on the territory throughout dependence, 6 involved late broods (hatched after 10 July). The fact that females left the breeding site with fledglings throughout the breeding season may be associated with the greater frequency with which females (compared to males) left the site following nest failure (see Chapters 30 and 33) and after breeding ended (Chapter 35).

Size of home range; discussion.—Of 50 family units (see Table 102) whose histories were best known, at least 19 (38%) probably rarely if ever left the parental territory; mean territory size was about 1.5 ha (see Chapter 29). Many units that moved appeared to take up a roughly defined new home range about the size of a breeding territory. However, the female-led units that moved just after nest-leaving and gradually drew farther away apparently had no home range during most or all of the period of dependence.

The high proportion of units never seen any considerable distance from the territory reinforces the suggestion (p. 324) that the parent determined the unit's

general course and the extent of its wanderings. Assuming that fledglings had no attachment to the parental home range, had adults followed fledglings much more dispersal would be expected. The fact that fledglings left the parental home range when they became independent suggests absence of site attachment, although conceivably an attachment had existed earlier but had come to an end.

HELPERS

Adult males.—A male once fed a fledgling not its own, and seven other males carried food into thickets in which young not their own were begging (experimental cases, p. 234, are not included). Three of these eight males were trespassing on the territory of the fledglings' father; their previous histories were unknown. Two others were banded trespassers; both had incubating females, and one had fed nestlings in an earlier nest of its own, which had failed. The remaining three males were on their own territories, into which the fledglings had been led by their mothers. One of these last three males had no young and probably no mate, and may have had no previous experience in feeding young that season; the histories of the other two were unknown.

In addition to the foregoing cases, a number of males followed fledglings so persistently that I suspected them of helping; but it was not clear whether they were interested in the fledglings or in the females feeding them. One unmated male onto whose territory a female-led unit moved followed the female persistently for 18 days, but I never saw him feed her young (see also p. 310).

In a case somewhat resembling helping, a male tended a fledgling Brown-headed Cowbird that had moved onto his territory from an adjoining Prairie Warbler territory.

Immature birds.—Independent immature birds sometimes attached themselves to family units and stayed with them for several days, at times displaying interest in the dependent young. Once one went through food delivering motions toward a fledgling, but I could not be sure that food passed.

CHAPTER 29

PRAIRIE WARBLER TERRITORIES AND THE MOVEMENTS OF MALES ON THEIR TERRITORIES

CHARACTERISTICS OF TERRITORIES, OTHER THAN SIZE

Territories were Type A (Hinde 1956: 342). Boundaries separating two territories are "interior"; others are "exterior." Most males with big territories confined a large share of their activities to only a part of the territory, on which the nest was located; when the nest failed, the center of attention shifted to the site of the replacement nest. Such males probably visited the less-used part of their land on most days, but possibly not much more often than they explored (see Chapter 30; compare Walkinshaw 1953, Meanley 1971: 48–50). Odum and Kuenzler's (1955) terms "maximum territory" and "utilized territory" will be used to differentiate a male's total and his temporarily preferred land. "Territory" when used alone refers to the maximum territory.

I studied 60 territories on the University Farm between 1952 and 1956, and 111 on the Griffey Tract between 1957 and 1965. Many at the University Farm were in fields large enough for only one male or were shaped in ways that dictated territory configurations (see Fig. 1). As a result some University Farm territories were the same every year, which was not true at Griffey. Because only the Griffey data are independent, only they will be tested statistically in most cases.

Figure 33 shows arrangements of maximum territories in selected Griffey fields and illustrates a number of points discussed below.

Boundary stability.—Territory boundaries were somewhat flexible. Males often fought for a few square meters that appeared to have no special features but readily abandoned other land that looked indistinguishable.

About 30–40% of Griffey males shifted maximum territory boundaries somewhat during the season. Shifts occurred in at least four circumstances: (1) When a male disappeared before breeding ended, neighbors often expanded into all or part of his land. (2) Several late-arrival males carved out territories from those of neighbors. (3) Occasionally females built nests outside mates' territories, usually on vacant land but four times on utilized territories of neighbors; this led to fighting and extension of the mate's boundary to include the nest (see pp. 40, 134). (4) When a utilized territory lay at one end of the maximum territory, a male might allow a neighbor to take over part of the unutilized land (compare Kluijver's 1951: 21–27 "domicile"). Such concessions, occasionally amounting to as much as 0.4 ha, often were temporary, with the males reverting to the former boundary if utilized territories changed.

Nature of exterior boundaries.—Prairie Warblers rarely left the shrubby fields; woods, pastures, and cultivated areas therefore formed most exterior boundaries. In early spring when food probably was still scanty (Chapter 4) birds of both

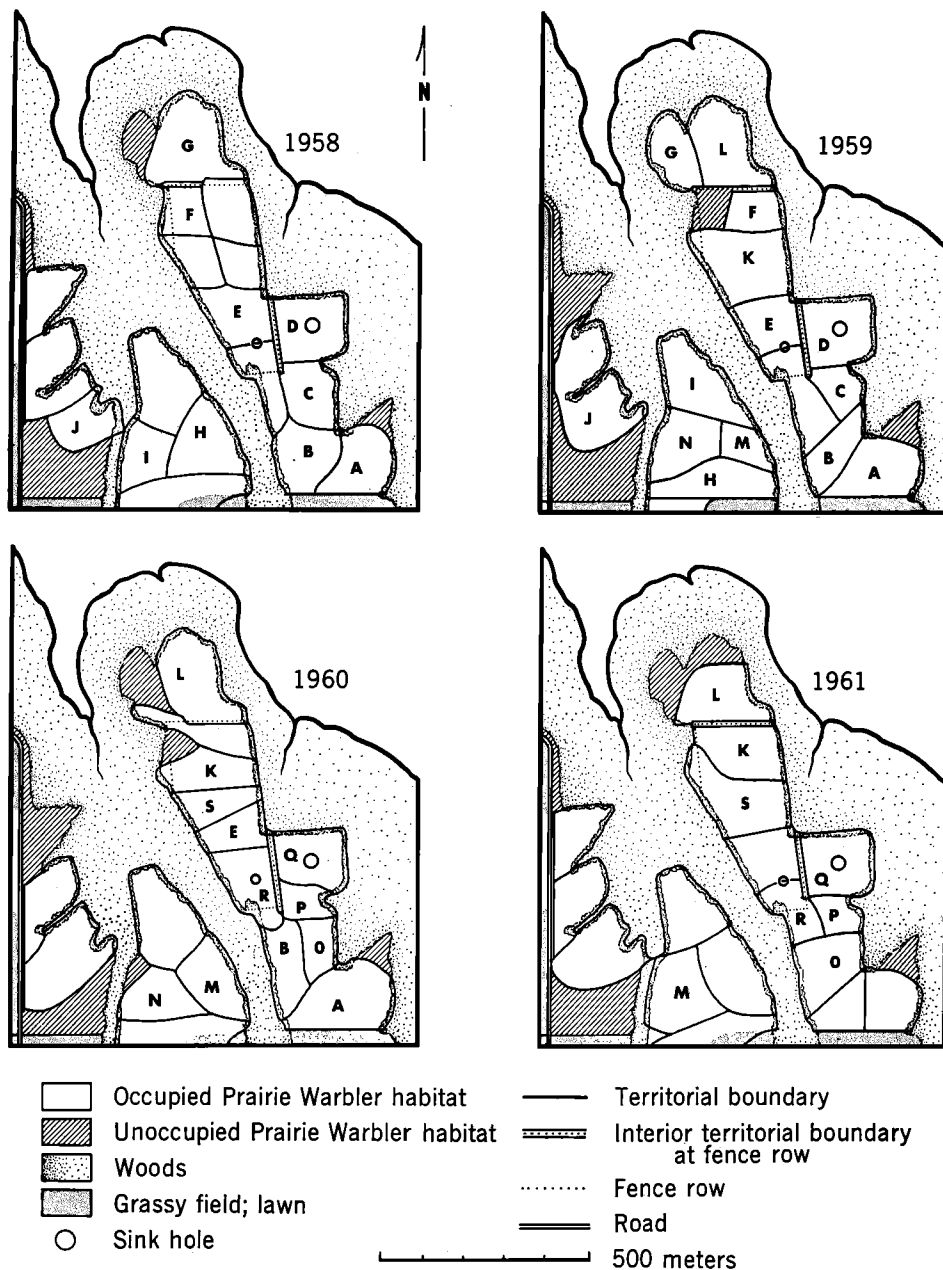


FIGURE 33. Configurations of territories on the principal Griffey fields, 1958–1961. Letters refer to individual male Prairie Warblers present in 2 or more years and the territories they held in those years; note the extent to which territory lines of such individuals changed.

sexes sometimes foraged in the woods canopy, and females occasionally built nests at the edge of the woods or even several meters within it (see p. 134).

Sometimes (78 of 171 territories) land lying beyond an exterior boundary was suitable Prairie Warbler habitat but was rarely or never entered by the

territorial male. Such unclaimed land always was located between the territory and woods or other unacceptable habitat. Presumably the males in these cases had all the space they needed; the absence of threat (neighbors) from the direction of the uninhabited area may have been a factor in leaving it outside the territory.

Nature of interior boundaries.—Interior boundaries were frequently zones about 10 m wide which both neighbors entered regularly. When males met, they often engaged in low-intensity fighting. Such co-owned zones were usually tree rows along old fences; reasons for this are suggested below. In the absence of tree rows some males fought repeatedly at one or two isolated points of their line but left the rest as a vaguely defined zone.

I could detect three factors that affected locations of interior boundaries: Nest placement was one, as already discussed. The others were conspicuous vegetational features and, occasionally between former neighbors, lines of the preceding year.

Vegetational features were most important. Taller tree rows along old fence lines and small streams and gulleys were perennial bounds or zones, regardless of changes in occupants of territories (see Fig. 33). In a revealing case, a male whose east boundary in 1957 was a tree row returned in 1958 and extended his territory to include land east of that row; when all territories around him had been settled and their lines adjusted, the tree row had become his western boundary. The apparent reason for the importance of trees taller than their surroundings was that males preferred to sing and keep watch from them; such trees overlooked both the singer's own and adjoining territories. Thus neighbors on each side of a tree row evidently had strong and equal incentive to fight for the right to enter the row but little incentive to go beyond; it became a shared zone. Tall trees in and around sinkholes either served as centers of territories or, like tree rows, were claimed by more than one male and became common property (see Fig. 33).

Vegetation also sometimes determined interior boundaries in a very different way: The less desirable the land in the middle of a large field, the more likely it would be a boundary (compare Armstrong 1955: 43). To illustrate, an eroded strip down the middle of a field supported few shrubs and forbs and therefore contained few perches and nest sites and probably little food. Year after year territories met along this strip, although neighbors did not enter it often; it evidently was not worth having and became a boundary by default.

A few boundaries were adhered to for 2–3 years for no apparent reason except that former neighbors seemed to accept an arrangement reached in prior seasons (compare pp. 40–41). However, most males did not take up precisely the territory of the preceding year (see Figs. 33 and p. 331). Thus, one male was perennially the first Prairie Warbler to arrive in spring (p. 29); he evidently took the land he wanted, always in the same field, and left his neighbors to work themselves in around him.

Shape of territories.—Almost all maximum territories were roughly rectangular or oval. When two lines crossing at approximately right angles were drawn on territory maps, most territories could be classed as square (lines approximately

TABLE 105
STRUCTURE OF VEGETATION¹ ON 171 TERRITORIES ACCORDING TO SECTION
OF STUDY AREA

	Rank 1	Rank 2	Rank 3	Rank 4	Median ²
Griffey Tract					
Tree height	39	62	10	—	1.8
Tree cover	1	23	65	22	3.0
Shrub cover	2	72	36	1	2.3
Ground cover	34	46	31	—	2.0
University Farm					
Tree height	19	29	12	—	1.9
Tree cover	14	17	24	5	2.4
Shrub cover	2	3	28	27	3.4
Ground cover	15	34	11	—	1.9

¹ Meanings of terms and ranks are described on pages 330–331.

² Note that scales of ranks were not based on equal intervals; see pages 330–331.

equally long), oblong (one line about 1.5 times longer), or elongated (one line more than 1.5 times longer). The terms are not intended to suggest straight boundaries or right-angled corners. Nearly all utilized territories were square, and utilized-territory shape will not be referred to again.

Shapes of territories were recorded as of dates used for analysis of size (p. 331); i.e. later changes were ignored.

Among 171 cases, 115 territories (67%) were square, 48 (28%) oblong, and 8 (5%) elongated. Of 111 Griffey cases, 68 territories were square (61%), 36 oblong (32%), and 7 elongated (6%).

Three males held two disjunct territories simultaneously, with a female on each (see p. 345). Another male's territory consisted for a few days of two parts touching at corners like squares on a chess board, conforming to the shapes of clearings in a woods (compare Meanley 1971: 48). He soon enlarged his area in one clearing and withdrew from the other. Still another unusual territory was a 20 × 475 m strip of shrubland between a cultivated field and a woods. The male disappeared after 3 weeks, without having obtained a female; compare the shapes of territories in certain dunes (p. 523).

Vegetation.—I classified the 171 territories according to four vegetational parameters, subdividing each parameter into several ranks. Percentages, heights, areas, etc., are approximate.

1. Tree height: Ranking was according to the highest trees in view of their apparent special importance (see p. 329); trees on boundaries were ignored because nearly all territories had some large boundary trees. Territories with trees taller than about 13 m were ranked 1; 6–13 m, 2; below 6 m, 3.

2. Tree cover: This percentage was estimated on the basis of the horizontal area of the crowns of trees at the point at which that area was greatest; total area of such tree cover was estimated as a percentage of the area of the territory. Cover above 50% ranked 1; 50–26%, 2; 25–6%, 3; 5–0%, 4.

3. Shrub cover: Shrubs included woody plants other than trees and also trees less than about 2 m tall. Territories more than 50% covered ranked 1; 50–25%, 2; 24–10%, 3; 9–0%, 4.

4. Bare ground: This category measured recent erosion. Territories with no bare ground ranked 1; 1–10%, 2; 11–20%, 3.

Table 105 summarizes rankings, suggests the configuration of the vegetation of the study area, and reveals differences between the Griffey Tract and the University Farm. The latter was more tree-covered and supported much less shrub growth; these differences can be related to differences in nest placement on the tracts (Chapter 15).

Number of adjoining males.—The following shows the number of territorial males along boundaries of the 171 territories: 0 males, 17 territories (10%); 1 male, 56 (33%); 2 males, 49 (29%); 3 males, 34 (20%); 4 males, 15 (9%). The median is 1.8, the mean 1.9 (SD 1.1). The considerable difference between the University Farm (mean 1.1) and the Griffey Tract (mean 2.3) is attributable to the small sizes of some clearings on the University Farm and to the long, narrow shapes of others (see Fig. 1).

Extent of internal boundaries.—Closely related to the foregoing point is the proportion of boundary that was internal. I estimated this in units of 60°, ranking isolated territories 1, those with 1–60° of internal boundary, 2, etc.

Differences between the University Farm and the Griffey Tract were great, and only the Griffey details are presented: rank 1, 20 territories (12%); 2, 27 (16%); 3, 39 (23%); 4, 38 (22%); 5, 11 (6%); 6, 30 (18%); 7, 6 (4%). For these 111 cases the median is 4.2; for 60 cases from the University Farm it is 2.8.

Extent of peripheral woods.—By the method just described I classified territories according to their contact with woods. Details for Griffey follow: rank 1 (i.e. least contact), 9 territories (5%); 2, 20 (12%); 3, 72 (42%); 4, 46 (27%); 5, 12 (7%); 6, 9 (5%); 7, 3 (2%). For these 111 cases the median is 3.2; for 60 cases from the University Farm it is 3.6.

Extent of other peripheral conditions.—All peripheral conditions other than woods and adjoining Prairie Warbler territories were ranked in a residual category. For Griffey, ranks were 1, 72 territories (42%); 2, 49, (29%); 3, 23 (14%); 4, 11 (6%); 5, 9 (5%); 6, 5 (3%); 7, 2 (1%). For these 111 cases the median is 1.4; for 60 cases from the University Farm it is 2.6.

SIZE OF TERRITORIES

Daily sightings (often several per day) of each male were recorded and plotted later on maps. Size is stated as of mid- to late May, when the number of occupied territories was greatest (Chapter 31). Zones of overlap were divided between the males involved. I estimated the locations of interior lines at which fighting was not observed.

Twenty-one banded males at Griffey provided data in 2 successive years. In the second year territories of 10 males increased more than 0.2 ha, and those of 8 males decreased at least 0.2 ha; in 3 cases there was no change. This points to independence of sizes from year to year.

On both the University Farm and the Griffey Tract some males had utilized territories, whereas others apparently used their full territories at all times; I lacked the necessary information for still others. Measurements of utilized territories are not as reliable as those of maximum territories; utilized lines were less

defined by fighting or unsuitable vegetation, and observations were fewer because utilization was temporary.

Maximum territories.—Extreme sizes were 3.5 and 0.4 ha; the mean (171 cases) is 1.56 ha (SD 0.65 ha). Extremes at Griffey were 3.5 and 0.5 ha; the mean (111 cases) was 1.62 ha (SD 0.72 ha). Extremes at the University Farm were 2.4 and 0.4 ha; the mean (60 cases) was 1.47 ha (SD 0.47 ha).

Utilized territories.—For the 24 University Farm males that had utilized territories, extremes were 1.4 and 1.0 ha; the mean was 1.09 ha (SD 0.18 ha). The mean maximum territory of these same birds was 1.75 ha (SD 0.42 ha), significantly larger than the utilized mean ($P < 0.001$). The mean size of the 24 utilized territories can be compared with the mean size of territories of 21 University Farm males that used all their land at all times (1.21 ha; SD 0.37 ha; extremes 1.8 and 0.4 ha); the difference is not significant. To obtain the area actually used at any one time by University Farm males, I pooled data for the utilized territories of the 24 males that had them and for the territories of the 21 males that had no inner utilized areas; the mean is 1.16 ha (SD 0.28 ha).

On the Griffey Tract, 54 males had utilized territories ranging from 2.8 to 0.7 ha; the mean was 1.21 ha (SD 0.38 ha). The mean maximum territory of these birds was 1.87 ha (SD 0.61 ha). For the 41 males that used their full territories at all times, extreme sizes were 1.6 and 0.5 ha; the mean was 1.02 ha (SD 0.33 ha), which differs from the mean of the 54 utilized territories; $t = 2.55$; $df = 93$; $P < 0.025$. Pooling the utilized territories of the 54 males and the full territories of the 41 males that had no inner utilized area gives an estimate of the area in daily use at Griffey; the mean is 1.13 ha (SD 0.37 ha).

Sizes of territories elsewhere.—At some of the population densities shown in Table 1, Prairie Warblers must occupy territories much smaller than those just described. Robbins *et al.* (1947) report 85 pairs per 40 ha in dry scrub in Maryland, a mean territory size of 0.47 ha if every part of the census tract was occupied. Schnell's (1963) discovery of a pair of Prairie Warblers nesting on a Georgia island 0.24 ha in area is of interest in view of a similar island effect in other species (Beer *et al.* 1956).

Territories adjoining unoccupied shrub land.—Sizes of maximum territories that adjoined unoccupied Prairie Warbler habitat suggest the area males would take possession when unlimited space was available to them. Extremes at Griffey were 3.5 ha and 0.6 ha; the mean (39 cases) was 2.16 ha (SD 0.73 ha). At the University Farm extremes were 2.4 and 0.4 ha; the mean (also 39 cases) was 1.47 ha (SD 0.47 ha). I have no explanation for the great difference between tracts.

Territory size and population density.—A long-term decline in numbers of Prairie Warblers on the Griffey Tract (Chapter 38) evidently was associated with successional changes, and territory size increased as the population decreased. Extreme sizes in high-density years (1957–1959) were 2.8 and 0.6 ha; the mean of 30 cases is 1.30 ha (SD 0.68 ha). In low-density years (1961–1962) extremes were 3.5 and 0.9 ha; the mean of 20 cases is 2.26 ha (SD 0.93 ha). Comparing the two classes of years, $t = 4.22$; $df = 48$; $P < 0.001$. This evidence of an association between density and territory size is reinforced by unsystematic observations

made after the study ended. Fewer males bred in 1970 than in any previous year, and sizes of maximum territories appeared to be 2.4–4.0 ha.

Territory size and age of male.—Old males probably had larger territories than yearlings. At Griffey I knew the sizes of 47 territories of males banded as adults in earlier years and of 23 males known or believed to be 1 year old. Extreme sizes for old males were 3.5 and 0.6 ha (mean 1.73 ha, SD 0.71 ha) and for yearlings 2.8 and 0.5 ha (mean 1.37 ha, SD 0.62 ha); $t = 2.07$; $df = 68$; $P < 0.05$. This difference emerged in spite of two factors that would tend to conceal it: The yearling sample may have included a few old birds (see p. 22), and the territories of old males were adjoined by more neighbors (mean 2.5) than those of yearlings (mean 2.0). As will be seen below, size and number of neighbors were negatively correlated.

The smaller territories of yearlings may have resulted from their later arrival in spring migration (Chapter 3); they confronted males whose claims based on previous years were already reinforced by occupation in the current year. Unusually small territories were invariably those of 1-year-old males that had arrived quite late.

Territory size and peripheral conditions.—For the 111 Griffey territories, size decreased as number of abutting males increased (mean when no neighbors, 2.1 ha; 1 neighbor, 2.3 ha; 2 neighbors, 1.7 ha; 3 neighbors, 1.3 ha; 4 neighbors, 1.1 ha). I tested 87 cases of size and number of neighbors for association, using Spearman's rank-difference method; $r_s = -0.426$; $t = 4.34$; $df = 85$; $P < 0.001$. To investigate whether this correlation simply reflected the inverse relation between territory size and annual population density I made separate analyses of territory size (Spearman's rank correlation) in years of high and low density. In high-density years, $r_s = -0.37$; $N = 30$; $P < 0.05$; in low-density years, $r_s = -0.62$; $N = 20$; $P < 0.01$. It therefore appears that the correlation is at least partly independent of annual density.

I also tested territory size against proportion of periphery consisting of internal boundaries, using Spearman's rank-difference method; $r_s = -0.62$; $t = 7.24$; $df = 85$; $P < 0.001$. Did number of neighbors and extent of internal boundaries have independent effects on size? I obtained Kendall's rank correlation coefficients using the same 87 data. For size and extent of peripheral contact, $\tau = -0.483$; for extent of peripheral contact and number of adjoining males, $\tau = 0.737$; for size and number of adjoining males, $\tau = -0.416$. Kendall's partial rank correlation coefficient ($\tau_{xy.z}$) for size and peripheral contact (effect of number of neighbors being held constant) = -0.287 , a value considerably smaller than the coefficient (-0.483) when effect of number of adjoining males is not partialled out. When peripheral contact is held constant and the relationship of size and number of males is correlated, the partial correlation coefficient is -0.101 (compare -0.416 , above). Thus the correlation between size and number of males seems largely dependent upon extent of peripheral contact, with the number of males involved of minor or of no importance (see Erickson 1938: 279–280, Armstrong 1955: 44, Krebs 1971: 17–19).

Territory size and vegetation.—As stated on page 330, lowest ranks were assigned to densest and highest vegetation, which requires that the sign of correlation coef-

TABLE 106
TERRITORY SIZE, ACCORDING TO FORM OF SEXUAL BOND¹ ON TERRITORY

Sexual bond	Maximum territory ^{2, 3}			Utilized territory ^{2, 3}		
	N	Mean, ha	SD	N	Mean, ha	SD
Polygyny	14	2.00	0.80	13	1.43	0.59
Season-long monogamy	49	1.59	0.52	44	1.13	0.27
Successive monogamy	14	1.46	0.96	12	1.03	0.32
Short-term monogamy	19	1.39	0.69	18	1.01	0.37

¹ For definitions, see text, this page.

² For definitions, see page 327. When males had no inner utilized territory, the area of the territory is included both in samples of maximum territories and utilized territories.

³ Data are from the Griffey Tract only.

ficients be reversed. In the following and all other correlations reported, the sign has been changed to reflect the true relationship.

I obtained Spearman's rank-difference coefficients and Kendall's rank coefficients between territory size (87 cases at Griffey) and all vegetational parameters. Both maximum and utilized territory size were tested; if a male had no inner utilized territory, I included the size of his full territory in the samples for both maximum and utilized. The only two significant correlations, both positive, were between maximum territory size and tree height (z -value of $\tau = 3.447$; $P < 0.001$) and maximum territory size and shrub coverage ($z = 2.260$; $P = 0.024$). Discussion is postponed until presentation of the relationship of territory size and form of pair bond (pp. 335–336).

Individual differences.—It is not clear whether individuals were consistent in holding large or small territories in successive years; the few data suggest they tended to be consistent. Because yearlings probably had smaller territories than old birds, I considered only the 15 males for which there were data from at least 3 seasons and ignored the first, possibly yearling, season. In view of the long-term increase in territory sizes with declining density, a male's territory size was compared with the mean size for the same year. Divergence of 0.2 ha or less was treated as no different from that mean.

(1) Two males held larger than average territories in 2 successive years, another in 3 successive years. (2) One held a smaller than average territory in 2 successive years, another in 3 successive years. (3) Six had territories of mean size in 1 year and deviated in another. A seventh twice held mean-size territories and twice larger. (4) Two birds were entirely inconsistent, holding small territories in 1 year, large in another.

Territory size and form of sexual bond.—Both maximum- and utilized-territory sizes at Griffey varied in association with the kind of sexual bond formed on the territories. When a male used his full territory at all times I treated it as both utilized and maximum; if I was uncertain on the point, I omitted his case from the sample of utilized territories.

Sexual bonds are described in Chapter 31. Four classes were compared for present purposes: (1) polygyny on one territory, (2) season-long monogamy, (3) successive monogamy in which a male remained on one territory all season and had more than one mate in succession there, and (4) short-term monogamy that started at the beginning of the season and ended before 25 June.

TABLE 107
ANALYSIS OF VARIANCE OF TERRITORY SIZES, ACCORDING TO FORM OF
SEXUAL BOND ON TERRITORY¹

Source	Maximum territory				Utilized territory			
	Sum of squares ²	df	Mean square ²	F	Sum of squares ²	df	Mean square ²	F
Between groups	203.528	3	67.843	2.45	96.361	3	32.120	4.06
Within groups	2547.768	92	27.693		656.020	83	7.904	
Total	2751.296	95			752.381	86		

¹ See Table 106 for descriptive data.

² Original measurements were in acres, and statistics in this table are the same.

Territories of polygynous males were largest, with a progressive reduction through season-long, successive, and short-term monogamy (Table 106). In analyses of variance for maximum territories F is about at 5% (Table 107); for utilized territories F exceeds the 1% point. Mean maximum size for polygynous males is significantly different from the other three means (Duncan's new multiple range 5% test). The latter means are homogeneous, but the gradient from season-long monogamy to short-term monogamy, i.e. from males most successful in retaining mates to males least successful, suggests that additional data would show differences. Testing utilized territories, the mean size for polygynous males differs from those for monogamous males at the 1% level; means for all forms of monogamy are homogeneous in a 5% test. (Note that polygyny did not appear to occur more frequently on some parts of the study area than on others.)

The number of days per season that females devoted to reproduction on Griffey territories varied according to form of sexual bond on the territory (see Chapter 31), with most female days spent on territories of polygynists, next most on those of season-long monogamists, and fewest on those of short-term monogamists. This order is identical, of course, with the order of territory size according to pair bond. Further, mean production of fledglings per territory also varied in the same order. I therefore ranked 87 Griffey territories from 1 to 4, with the territory on which there was polygyny as 1, season-long monogamy 2, successive monogamy 3, and short-term monogamy 4. Spearman's rank-difference and Kendall's rank correlation tests reveal that the only significant correlation between rank of sexual bond and rank of parameters of vegetation was the correlation between bond and tree height; $\tau = 0.175$; $z = 2.40$; $P = 0.016$. I then used Kendall's partial rank-correlation method to investigate for an independent relationship between bond and territory size and between bond and tree height. τ for bond and maximum territory size (0.245) changed to 0.211 when effect of tree height was partialled out; τ for the correlation between bond and tree height (0.175) became 0.121 when the effect of territory size was partialled out. Neither change is great, and the correlations may be independent; at least, the one between pair bond and maximum territory size appears direct and real.

To attempt to interpret: (1) Maximum territory size was probably positively associated with success in attracting and keeping females. (2) Because males with two females were attentive to both (e.g. pp. 147-148; see also p. 368) and mates of polygynists appeared to build their nests some distance apart (Chapter 15),

TABLE 108
SIZE OF MAXIMUM TERRITORIES,¹ ACCORDING TO SHAPE²

Descriptive statistics			
Shape	N	Mean, ha	SD
Square	68	1.45	0.66
Oblong	36	1.84	0.69
Elongated	7	2.06	1.02

Analysis of variance				
Source	Sum of squares ³	df	Mean square ³	F
Between groups	295.440	2	147.720	5.01
Within groups	3187.187	108	29.511	
Total	3482.627	110		

¹ The term is defined on page 327. Data are from the Griffey Tract only.

² Terms designating shape are defined on pages 329–330.

³ Original measurements were in acres, and these statistics are the same.

polygynous males would tend to utilize a larger area than monogamous males holding territories of equal size. Thus I suggest that a large maximum territory enhanced chances of acquiring a second female, whose acquisition led to enlargement of the utilized territory. (3) As for the relationships of tree height, maximum territory size, and pair bond, the probability that large trees would be present may have increased simply because territory size increased. However, the very strong correlation ($P < 0.001$) between tree height and territory size suggests either that males with big trees needed more land or that their ability to hold more land was improved by the presence of such trees. The latter seems much more probable; from a tall tree a bird could survey his territory and perhaps advertise more effectively (see pp. 329, 338–339). If tree height was independently associated with form of sex bond, it is possible that tall trees entered into female evaluation of the territory or its owner.

Territory size and shape of territory.—At Griffey, maximum territory size was correlated with shape, all indications being that territories were square when area was reduced and space was at a premium. Shape was not associated with any ranked vegetational parameters. (As noted, utilized territories were all about the same shape.) Table 108 shows mean size per shape, with an analysis of variance; $F = 5.01$ and $P < 0.01$. Mean size of square territories differed from the other means, which were homogeneous (Duncan's new multiple-range test, 5% level; all means homogeneous in a 1% test).

Tests of independence of shape and number of adjoining males were non-significant ($0.10 > P > 0.05$), but square territories were somewhat less frequent than expected when number of neighbors was 0, 1, or 2 and more frequent when the number was 3 or 4. Other statistics (see the following paragraph) make it likely that when neighbors were numerous males took up compact, i.e. square, territories. The energy cost of defending such territories is probably lower, because from a central perch a male could more readily survey and make his song heard over all his land. In contrast, a male singing in the middle of a long narrow territory might be inaudible at some boundaries and audible much farther than necessary at others. Thus, shape may have responded to population

density in the same way that size apparently responded to increasing contact with males on the periphery, and for similar reasons.

Seeming to support the foregoing point are these data: (1) Only 18 of 68 (26%) square territories adjoined unoccupied Prairie Warbler habitat, whereas 21 of 43 (49%) oblong and elongated territories did so; adj. Chi-square = 4.7; $df = 1$; $P < 0.05$. (2) In years when population density was high five territories were oblong or elongated and 25 were square; when density was low 10 were oblong and elongated, and 10 were square; adj. Chi-square = 4.9; $df = 1$; $P < 0.05$. (3) Males with utilized territories inside maximum territories obviously had land that they did not need to use intensively. Of 54 such males at Griffey, maximum territories of 28 (52%) were square; of 41 males without inner utilized territories, territories of 31 (68%) were square; adj. Chi-square = 4.6; $df = 1$; $P < 0.05$.

MOVEMENTS AND TERRITORIAL ACTIVITIES OF MALES, ACCORDING TO STAGE OF BREEDING CYCLE

This section covers stages of breeding when male behavior on the territory was entirely or largely independent of relations with a mate and/or offspring. Behavior and movements at other times were affected by interactions with female and progeny and are described in chapters devoted to the relevant stages of reproduction.

Pre-pair-formation period.—Characteristic behavior of unmated territorial males at all dates consisted of perching at or near the highest available treetops, flying back and forth between interior or potentially interior boundaries (doing so less frequently when boundaries could be overlooked from midterritory), and singing steadily and frequently. Obviously, occasional males did not conform to this pattern. A typical case will be described.

On 1, 2, and 3 May, in fair weather, I recorded a male's movements for 1.5–2 hours each day, beginning at dawn and excluding brief periods when he left the territory. The territory was square, 1.6 ha; it was bounded by an occupied territory, a shrubby field that a male occupied a few days later, a woods, and a grassy field. A few tall trees were scattered over it rather uniformly; shrubs and small trees were sparse. Behavior each morning was fairly similar, and many data are pooled. *Heights:* The male spent 16% of 242 min below 2 m; percentages for successively higher 2-m intervals were 13, 9, 11, 19, and 32; therefore about 50% was spent at or above 8 m, near the tops of larger trees. *Allocation of time:* He perched, sang, and surveyed the territory 83% of the total time, sometimes preening between songs; 14% of the time he foraged without interrupting his singing; the rest (3%) of the time he moved between perches, chased small passerines, and fought his neighbor at their boundary. Most perching and singing were at higher elevations, most sustained foraging at lower. He sang 794 songs in 242 min (mean 3.3/min). *Movements and intervals between them:* On 1 and 2 May, I recorded 47 flights from one tree or shrub to another. Extreme distances covered were about 2 and 330 m, the latter to a point outside the territory; the mean was 85 m (SD 79 m). Extreme intervals between moves were about 1 and 12 min; the mean was 5.5 min (SD 3.6 min). Thus, on these

2 days the male tended to stay in one tree for a considerable time, then to fly far, usually halfway across the territory. On 3 May his behavior differed. He concentrated on the center of his territory, hardly leaving it during 69 min, perching high and looking around as usual. *Coverage of territory and distances traversed:* On 1 and 2 May he crossed the territory several times per hour and visited and sang equally frequently at the two boundaries abutting Prairie Warbler habitat; e.g. he reached each of these boundaries four times during 120 min on 1 May. He also sang in midterritory; therefore his plotted positions are rather evenly distributed (compare Ickes and Ficken 1970: Fig. 1). On 1 May the total distance traversed in 120 min was about 1750 m, on 2 May in 70 min about 1650 m. His concentration on midterritory on 3 May made it difficult to estimate the distance he covered; probably it was about 300 m in 69 min (until a female appeared at 0630 and caused his behavior to change).

Incubation period.—During day-long nest watches I recorded substantially all songs of territorial males; on compact territories I could estimate distances with some accuracy, and I observed or estimated all locations of males when they sang. I plotted song locations at all hours except at dawn (see the following paragraph); males moved across and around the full territory and sang from perches rather evenly distributed over the area (compare Ickes and Ficken 1970: 173 and Fig. 2). There appeared to be no pattern of movement from one day to the next and little tendency to prefer parts of the territory at certain hours (compare Weeden 1965). However, as described below, some males had one or more song posts and tended to spend more of their time at these. Casual observations suggest that locations of males during their intervals of silence were distributed about the same as during their periods of singing, i.e. were scattered over the full territory.

Some males—possibly most—usually or always sang at dawn from a restricted area. Dawn singing locations tended to be the same each day and were not necessarily in midterritory or near the nest; e.g. one male sang each dawn in a corner of his large territory.

SONG POSTS

Many males, possibly about half, showed a preference for one or more trees from which to sing. Numbers and locations of song posts appeared to be determined by territory shape and size, position of trees relative to territories of neighbors, structure and height of surrounding vegetation, and location of the nest. Some preferences continued all season; others changed when utilized territory changed. Use of song posts was most pronounced in unmated birds and birds with incubating mates, i.e. during stages when the male's movements and locations were least influenced by other Prairie Warblers on his territory.

Song trees were almost always considerably higher than the surrounding vegetation and, as already indicated, many were the tallest on the territory. Very often the branch from which the male sang was dead (compare Mayfield 1960: 133), which presumably gave him a better view and also made him more conspicuous. Even when the only tall trees present were on exterior boundaries, hence least useful for overlooking neighbors, males often selected them; some posts were at

opposite ends of the territory. In smaller trees 6–10 m tall the singer usually perched within 1 m of the top; in taller trees tips of horizontal limbs in the top quarter were often used.

Considering that males obviously selected trees at least partly on the basis of the view they afforded, the term song post is not entirely apt; "lookout post" may be more descriptive. For example, a male once flew to his song post in mid-morning and for 8 min looked around alertly but in complete silence.

BIOLOGICAL SIGNIFICANCE OF PRAIRIE WARBLER'S TERRITORIALITY

Site for pair formation.—Indications are that the Prairie Warbler's territorial behavior functions first (see Hinde 1956: 354–357) to bring the male and female together, then minimizes outside interference while they are becoming familiar with each other. Differences in song frequency before and after pair formation (see Tables 11 and 12) and behavior of females when approaching unmated males (Chapter 10) imply the importance of song, a form of this species' territorial behavior, in causing the pair to meet.

As described on page 52, unmated territorial males often trespassed while pairs were forming on adjoining territories in spring. If territorial behavior had not already parceled out the land and set some restraints on such interference, pair formation would surely have proceeded much less efficiently than it did. Any delay in start of reproduction would shorten the breeding season. The importance of efficient use of time by birds exposed to heavy nest predation and potentially dependent on frequent renesting is indicated on page 93, as are advantages of bringing off young at an early date (see also pp. 398–399).

The visible behavior (see Chapter 10) of both sexes during the 2–3 days following their meeting reflects agonistic tendencies that had to be overcome; it seems clear that isolation from other Prairie Warblers would permit this process to run its course most rapidly. The female also probably needed time to learn her mate's vocalizations (see Chapter 8), one aspect of adjusting to him. If he were not faithful to a restricted site and did not exclude other males from it, that aspect would also be greatly complicated.

Pair formation continued all season (see Chapter 11), which may help explain why territorial behavior did not wane greatly once May had passed. But territoriality probably had other functions than those associated with pairing.

Defense against interference with nest building.—Territorial behavior permitted the female to build her nest with less molestation by neighboring males. Some evidence that it is advantageous to isolate nest building is the female's avoidance of sites near interior boundaries (Chapter 15). The fact that males enlarged their territories when females began to build outside them is also significant (compare Hinde 1956: 357), although obviously this enlargement was functional in other ways (e.g. in making it easier for males to feed their nestlings). Similarly, the male's great interest in his mate's nest building and his concession of parts of his territory remote from—but never near—the nest is some proof of the importance of isolating the building female. It was demonstrated frequently that building could not proceed efficiently with neighboring males nearby. In an especially suggestive case, a female abandoned a far-advanced fragment near an interior

boundary at which her mate had to fight off a neighbor almost constantly. Within 3–4 hours of abandoning she began a nest on the opposite side of the territory at an exterior boundary, strongly suggesting that she had not quit building the fragment because of any physiological deficiency on her part.

If interference with building is disadvantageous, the question remains whether it would occur if the male did not fight his neighbors when they approached. Why not let them watch? The probable answer is that the neighbors would not be passive spectators but would make sexual advances to the female; males usually courted any female near them, any time in the breeding season (e.g. pp. 328–329). Because females are receptive to copulation during nest building (see Table 26), pressure should be strong on the territory holder not to risk stolen copulations with his mate and the chance that he would expend his energy on rearing young carrying a neighbor's genes.

Exclusive feeding area.—Theoretical reasons (Horn 1968; see also Schoener 1968) and some circumstantial evidence exist for believing that the Prairie Warbler's territoriality maximizes food supply at the lowest energy cost. Food of the species, almost exclusively invertebrate (Chapter 39), is probably widespread and evenly and stably distributed during much or all of the breeding season, thus satisfying the conditions of Horn's (1968) model.

Adult Prairie Warblers obtain virtually all nestling food on the territory. Territory size did not change during the nestling interval (see p. 276; compare Stefanski 1967), but the territory could function as a preserve for obtaining food for young even though its area is defined earlier in reproduction (see Tinbergen 1936, Krebs 1971). Simply because Great Tits rarely forage for nestlings other than on the territory, Krebs concluded (1971: 16) that territory may have a "selective advantage in preserving a food supply for feeding the young."

There are suggestions that other aspects of the Prairie Warbler's spacing may have been dictated by feeding considerations: If mates of polygynous males avoided each other's nests in locating their own, as suggested (p. 135), such spacing may have been food-related. Young in well separated nests could be provided for at a lower energy expenditure, and nestlings could be brooded more of the time, if the food near a nest were exploited by only one female. The importance of a close, exclusive foraging preserve should be greater for the mate of a polygynist, because of the risk that she might receive less male assistance than a monogamist's mate receives (see Orians 1969). And in Chapter 39 it is shown that during nesting males and females, whatever the pair bond, foraged at different heights. One reason may have been that this simplified the female's tasks of providing for herself and performing parental duties and thus improved chances of reproducing.

Finally, the correlation among (1) maximum territory size, (2) male reproductive success, (3) form of pair bond, and (4) female days spent attempting to reproduce (this chapter and Chapter 31) means that food consumption per territory was greater on large territories. Evidence that these territories were richer or less rich in resources per unit area is lacking. It may be that acquisition of a larger food supply (i.e. greater area) was what made it possible for a male to improve his reproductive output and worthwhile to expend the energy to hold a bigger tract.

CHAPTER 30

EXTRATERRITORIAL ACTIVITIES AND MIDSEASON CHANGES OF LOCATION

MALE EXPLORATION

Routine trespasses are here distinguished from what looked like a different kind of behavior, explorations. Trespasses usually were brief, covered short distances, and probably occurred in most instances when the trespasser's attention was attracted by events on adjacent territories; trespasses regularly led to confrontations and fighting (see Chapter 7). In contrast, explorations covered considerable distances, lasted for minutes or hours rather than seconds, frequently appeared stealthy, and rarely led to observed encounters. Although the foregoing distinction may draw sharper lines than existed in fact, I saw 155 episodes conforming to the description of explorations; they bore little resemblance to the typical bickering, fighting, and encroaching of neighbors. Explorations as a normal form of behavior would only be detected in a population in which most males are color-banded, and the often rather secretive movements of explorers assure that many will be overlooked.

Approximate distances at which banded males were observed beyond their territories ranged between 50 m and 1.2 km; the mean was 280 m (data not normally distributed), the median 250 m. Dates were from arrival in April until the end of breeding in August. Times of day covered the full period of daylight. When the day is divided into equal intervals of 4 hours beginning at 0430, explorations were randomly distributed in relation to my time in the field, except that observed numbers were below expected between 1630 and 2030.

Some or all males probably left their territories as often as once per day, especially when their mates were incubating (see below). The highest number of explorations observed for one individual was 12 (7 May–11 June), at distances of 200–700 m from his territory. Three times I saw males during two different explorations on the same day.

Data on the duration of explorations are scanty. Eleven times after seeing a male leave his territory I waited for his return (as signaled by his beginning to sing), which usually occurred 15–60 min after his departure (mean 30 min). Once on 24 April, at 0705, I met a banded male 100 m from his territory and moving away from it, and I therefore went to the territory and waited for him. By 0840 he had not returned, and his neighbors were trespassing freely (note the date, at the beginning of the season). I left temporarily and went back at 1022; there was no sign of the male until at 1036 he began to sing and immediately evicted a trespasser. Thus this exploration may have lasted about 3.5 hours. Frequently during 1–2 hours on a territory I heard no song under circumstances when singing would have been expected, and I concluded the male was exploring. (See also the discussion of temporary midseason relocation, p. 344).

In 24 of 155 cases an explorer sang; if he was in unoccupied Prairie Warbler habitat, he usually did so repeatedly. Once a male sang on a territory until its

owner began to sing; the interloper immediately became silent and flew away into a woods. In about 30 cases Chek was called just before or during an exploration, in about 20 cases Tsip.

Frequently explorers gave an impression of stealth. Thus, a male sat motionless for 2 min while watching a territorial male as it sang; the explorer raised and lowered the crown feathers repeatedly (see p. 500); when the territorial male changed perches, the explorer followed as though shadowing. Tense, horizontal perching in evident readiness to fly and rapid scanning movements of the head characterized some explorers. Not all males behaved cryptically; one far from his territory at 1937 foraged rapidly and energetically (typical of foraging just before darkness; see pp. 489, 491) near the nest of the territorial male's mate.

Objects of explorers' attention.—Among 155 explorers, 123 seemed to be watching other Prairie Warblers or their nests; the remaining 32 were engaged in maintenance or other nonsocial behavior. Fifteen were not seen on the territory of any Prairie Warbler. In descending order of frequency, explorers on Prairie Warbler territories were apparently watching the following: nest building, 42 cases; activities of young out of the nest, 24; feeding of nestlings by a female, 17; incubating by a female, 10; courtship and pre-nest-building behavior, 9; advertising by a male, 7; miscellaneous Prairie Warbler activities, 7; Prairie Warbler nests during laying interval (no female in sight), 7. Seventeen explorers on Prairie Warbler territories were not observing the owners, their nests, or their young.

Special comment should be made on the interest that males have in nests and nesting activities of other pairs; four cases demonstrate this. (1) I caught seven males in traps or nets placed near nests on other males' territories. (2) During 2 days spent trying to catch an unbanded male near his nest, I caught 3 of his 4 neighbors before I finally caught him. (3) I put up a net to catch a female as she built. When I returned to the net I had her, her banded mate, and a banded male from a territory 450 m away; as I started to remove these birds, an unbanded male went to the nest and stood on its rim. (4) Eighteen times during my long nest watches (Chapters 17, 21, and 24) a male other than the territory owner went to within 2 m of the nest. One appeared to be watching the incubating female; his own mate was incubating 1100 m away.

Additional evidence that males were aware of the locations of nests and of the general situation on surrounding territories was abundant. Nest building often was observed by an audience of neighboring males, some of which kept abreast of events from high perches on the boundaries of their own territories, i.e. without trespassing or exploring. I could often predict what had happened or was happening on a territory by listening to the territorial male's vocalizations as I arrived, and these probably conveyed equivalent information to any Prairie Warbler within earshot.

During and after breeding, in 16 instances I discovered males on territories they had formerly occupied (Chapter 37), suggesting either that explorations are sometimes motivated by attraction to such sites or that explorers when near former territories stop and visit them.

Situations on explorers' territories.—Consideration of situations on territories of 105 exploring males may cast light on the behavior: female incubating, 39 cases; male unmated, 26; clutch being laid, 20; dependent young out of nest, 8;

nestlings in nest, 6; female building nest, 4; female about to build, 2. This distribution suggests that exploration was most frequent when opportunity to associate with a mate was limited. Possibly, too, the presence of young to be fed tended to keep males from leaving the territory; but in evaluating the low number of explorations by males with young it should be recalled that predators and cowbirds caused most nests to fail before hatching (see Chapter 33).

Exploration appeared unrelated to the degree of isolation of the territory: Neither number of singing males within earshot of their territories nor number of adjoining neighbors is correlated with the frequency with which I found individuals exploring.

Discussion; functions of exploration.—Explorations could play a role in the process of relocating to new territories, both before breeding begins (see Chapter 5) and in midseason (see below). Some relocations may have originated as explorations; the attractions of a place visited may have outweighed the impulse to return home. This suggestion is supported by a number of observations: (1) Most males relocated either before a mate was acquired in spring or after one was lost in midseason (see pp. 32, 344, 350); as just shown, lack of opportunity to associate with a female was also often associated with exploration. (2) Some explorers sang at normal territorial frequency on tracts not occupied by other males; relocating males did the same but remained to become owners of such tracts. (3) The many cases in which a male took over a new territory only temporarily (below) may not differ in kind from prolonged explorations; like explorers, these males then went back to their original territories. (4) Cases in which males held two separate territories simultaneously (see below and Chapter 31) may have arisen when these males were exploring; they may have found and taken over unoccupied sites but also have retained attachment to the original territory. (See also the discussion on p. 345.)

If exploration and relocation are related as suggested, then exploration functions in part as a dispersal mechanism, giving some acts of dispersal a trial-and-error and a conservative character: a suitable new site is found before the old one is abandoned. Even if no such direct relationship exists, acquaintance with the surrounding area, gained by exploring, could provide a basis for evaluating and comparing sites; this in turn could contribute indirectly to future relocation.

If exploration is related to the concurrent holding of two territories, it plays a role in the Prairie Warbler's polygyny (see pp. 354–355).

Numerous reports, for various species, tell of observations of supposed non-breeding or floating-surplus males. Thus Brewster (1885) recounts how Wayne refrained from collecting female Swainson's Warblers and their young in order to decoy "bachelor males"; once he obtained five males in succession near a single female. Exploring could account for many such observations, if the behavior is widespread. Kendeigh (1945, 1947: 73–75) in several parulids and Mayfield (1960: 47–48, 1962) in Kirtland's Warbler have observed behavior much resembling the Prairie Warbler's exploring, suggesting that exploring is more general than realized. Until further information is obtained, it seems unwarranted to assume that unidentified male passerines seen on other males' territories are members of a floating surplus; they may be explorers.

MALE RELOCATION OF TERRITORY

Changes of territory by males and of home range by females, other than those changes that occurred shortly after arrival on spring migration, were intimately associated with pair dissolution and therefore with the Prairie Warbler's mating system. For that reason many details of such changes are set out in the description of the mating system (Chapter 31).

Unless the contrary is stated, all references herein are to midseason movements to and from 135 territories that were the subject of special attention (see p. 348). Territories taken over after the beginning of the season (defined on p. 89) are classed as "gained in midseason" (see p. 349). Territories from which a male disappeared after a mate of his had nested there are considered "abandoned in midseason" if the disappearance occurred before 25 June; reasons for using that date are discussed on page 349. Boundary adjustments and encroachments on parts of evacuated territories are not regarded as relocations and are excluded from present consideration.

Permanent relocations onto study area.—Six territories that had been abandoned were taken over by new owners in the season in which abandoned, 3 times by unbanded newcomers to the study area and 3 times by banded study-area males. These acquisitions, the latest on 1 July, were followed by pair formation and nesting. Four additional males appeared in midseason on land that had not been occupied in that year, acquired mates, and remained for the rest of the season. Reasons for believing that most or all of these 10 males had relocated from territories elsewhere appear below. (In this and the following subsection, four males that acquired second territories in midseason without abandoning their first territories are included in the number that relocated.)

Temporary relocations onto study area.—Two banded males took up territories in midseason and abandoned them after relatively brief periods; both were birds that had moved off the study area, presumably having relocated, in earlier years. Twelve other temporary relocations to the area were by unbanded males. Some of the land occupied by this total of 14 males had been vacated earlier in the same season by territorial males; other land had not been held previously during the year.

The 14 temporary holdings lasted from 2 to 22 days; the approximate mean was 8 days (SD 6 days). Dates of arrival fell between 1 May and 14 July. None of these males acquired a mate, although some met females and courted them. Failure to gain a mate and failure to remain on the territory seem clearly related, considering that the 10 males (preceding subsection) whose relocations were permanent did acquire females. The importance of getting a mate as a factor causing a male to remain on a territory is further indicated by comparing the ratio of permanent and temporary moves at the beginning of the season (21 permanent: 4 temporary; see pp. 31–32) to the same ratio in midseason (10 permanent: 14 temporary). This seasonal difference ($P < 0.01$) is probably explained by variation in number of unmated females available for pairing at the two times; at the beginning of the season a male would be more likely to attract a mate arriving from migration, and his move would more likely be permanent.

Permanent disappearances (probable relocations) from study area.—Sixteen

males disappeared from the 135 territories between 10 May and 25 June. If tracts less thoroughly studied are included, the total is 22 territories left untenanted by 25 June, with 3 others abandoned between 26 June and 1 July. Some of these were later taken over by new males, as shown above. (Probably few if any males that disappeared in midseason died; some were seen in later years. See the discussions on pages 349–350 and 469 and note the significance of the data in the following paragraphs.)

Temporary disappearances from study area.—Temporary desertions of territory in midseason parallel temporary relocations in spring (see p. 31) and, as noted earlier, suggest a link between exploration and permanent relocation.

At least 11 banded males disappeared (early May to mid-July) from territories for 1 or more days and then returned; 6 cases lasted 3 days or longer. An especially informative case follows: A male lost a mate on 10 June; on 20 June he left the territory he had held for 3 years and moved 1 km to an unoccupied field, where he advertised steadily but without success until 9 July; he then returned to his original territory for the rest of the season. While holding the temporary territory he had also visited his original territory and advertised there briefly on 27 and 29 June. Had a female in breeding condition appeared on the temporary territory, it seems certain that a pair would have formed and the territory become permanent.

Simultaneous holding of two territories.—Four of the most interesting cases of midseason acquisition of territory involved no abandonment of territory. Each of four males in May or June took over a territory whose first tenant had disappeared; each obtained a mate there (in two cases the mate of the former owner) but continued also to hold the site occupied since the beginning of the season (see Mumford 1964: 22). One of the second territories acquired adjoined the male's original territory. Another male's two territories lay in different fields but were contiguous at their corners. The territories of the third were 100 m apart, separated by a wooded ravine. In the fourth case the second was 1300 m from the first, separated by woods which the male crossed at least once a day for 37 days or more.

In addition to apparently linking exploration to acquisition of territory, these cases seem intermediate between normal season-long site fidelity and normal mid-season relocation (see the following subsection; compare von Haartman 1949: 14–15, 1956: 469–473). They are also related to two instances of polygyny in which males enlarged territories by taking over sections of evacuated land, then obtained second females.

Successive holding of territories.—No banded male was found breeding on two territories successively in the same year; thus direct observation of a permanent midseason relocation is lacking. Nevertheless, on the basis of the behavior described above I believe it safe to assume that males changed territories permanently in midseason, just as they were directly observed to do shortly after arriving in spring (see Chapter 5). This is the clear implication of the case of the male that advertised from 20 June to 9 July before returning to his original territory. Further, acquiring a new territory in midseason without abandoning the original territory is more complex and improbable than is a permanent move from one location to another; since the former was observed, the latter, simpler behavior is expected.

Also, the behavior of females is probably relevant to that of males, in view of the general similarity between expressions of site fidelity by males and some females (see Chapter 37); as will be seen below, banded females were found breeding on two home ranges in succession in a single year. I therefore conclude that most males that came to the study area in midseason had held territories elsewhere and that most males that disappeared before the breeding season ended moved to territories off the area.

FEMALE MOVEMENTS

Permanent change of home range within study area.—Four banded females left first mates' territories in midseason (terms are defined as in the case of males, above) and paired with other males. Three were old and one was a yearling. Two moved (125 and 500 m) within 1–2 days of bringing off first broods; the other two moved after nest failures, leaving sites from which their mates had already disappeared. One of these latter two joined the adjacent male (making him polygynous) 125 m away, but the other passed through two territories and paired with an unmated male 520 m away. This last female disappeared from the study area about 16 June after a nest failed. Given the earliness of this date (see Chapter 34), she may have moved to yet a third male's territory.

Temporary changes of home range within study area.—Two females made temporary moves in midseason under identical circumstances: Each failed in an initial attempt to raise a second brood and next day was found (300 and 500 m away) being courted by a new male. Within two days each was back on the territory of her original mate, where she again attempted to raise a second brood.

Movements onto study area.—In midseason, 36 females moved to the study area and nested on the 135 territories; these birds had not bred there earlier in the year (some had incubation patches when they arrived; see p. 348). In addition, numerous females passed through the area. These latter did not restrict themselves to any location, and therefore it is impossible to liken their cases to those of the males that came to the area and temporarily became territorial. However, cases comparable to male temporary territoriality were provided by two females that appeared on the area (25 May and 7 June), behaved as though mated and worked on nests for about 2 days, but left these as fragments (Chapter 12) and deserted the males courting them.

Disappearance from study area.—Sixty-two females left the study area before 25 June, after having built at least one nest there. Seven had also arrived in midseason; their mates on the area probably were not their first of the year, and may not have been their last. Another female, as described above, had had two mates on the study area before she moved.

CHAPTER 31

MATING SYSTEM AND SEX RATIO

PROBLEMS AND METHODS

Sexual relationships of Prairie Warblers on the study area were diverse and often complex. Understanding of problems and methods will be aided by considering three cases.

1. Male A obtained a mate in April; she disappeared after a nest failure but was quickly replaced. The replacement female also left after a nest failure. Male A then obtained a third mate, which produced fledglings in July. Meanwhile, male A had taken possession of a second territory 1.3 km away; he commuted between his two territories at least once daily. The original owner of the second territory had disappeared, leaving an incubating mate; her nest soon failed and she became male A's mate, making him a polygynist. She too brought off young.

2. Male B held a large territory and acquired two females at the beginning of the season. The first nests of these females failed nearly simultaneously. At about that time newly arrived male C took over half of male B's territory and one of his mates; male C fathered (I assume) the eggs in this latter female's new nest. Male C then disappeared; male B reoccupied the territory, resumed his relationship with his former mate (becoming polygynous again), and fed the nestlings of male C.

3. Polygynous male D's territory adjoined that of monogamous male E. Male D was deserted by one mate on 28 June, by the other on 4 July. On 6 July the mate of male E brought off fledglings and next day, on a date at which most females were no longer capable of breeding (p. 423), she deserted her family and paired with male D. She built and laid in two more nests after forming this bond.

The difficulties of classifying Prairie Warbler sexual bonds and analyzing them quantitatively are these:

1. The mating status of many individuals changed during the season, sometimes repeatedly, and an adequate classification should identify bond(s) for the full season. The sexes must be treated separately; a bird of either sex could be monogamous for a season while its mate had multiple bonds.

2. Change in mating status often involved relocation to a new site, usually not on the study area. Midseason disappearance of many birds was paralleled by appearance of others, and consequently I obtained full-season histories of only a fraction of the individuals that bred on the area. Most members of this fraction were monogamous for the season; both in that respect and in their season-long site fidelity they are not a representative sample.

3. If the full season is the time unit being analyzed, it is important to know when an individual began and quit breeding. Individual variation in length of breeding season (see Chapter 34), in combination with movements to and from the

study area, often makes it impossible to be certain that a nest was a bird's last of the year.

4. In analyzing stability of the sexual bond it is desirable to differentiate disappearances caused by death from those caused by pair dissolution and movement to a new location. Some color-banded birds that disappeared were seen again after breeding ended or in another year, but most vanished permanently.

Use of histories of locations as basis for inferring histories of birds.—To obtain season-long units of information, I have compiled histories of territories. The kinds of sexual bonds formed in midseason by newcomers to these will imply the kinds of bonds formed by the birds that moved off the study area in midseason, unless frequencies of bonds formed on the study area differed from those in the surrounding region. It is conservative to assume that they did not differ, and the following facts tend to show that they did not: (1) Individuals banded in previous years sometimes returned in midseason of later years (e.g. see pp. 352, 463), suggesting that the region to which the study area supplied birds and from which it drew them was not large. The smaller its size, the greater the likelihood that the ecology and behavior of Prairie Warblers were the same throughout. (2) Six of seven females that I caught immediately after they arrived in midseason had fully developed incubation patches, indicating that they had previously laid eggs elsewhere (see pp. 195–196); the exception arrived at the end of May and was probably a late migrant. This proves that in the surrounding region some pair bonds terminated in midseason, just as some did on the study area. The existence of regional similarity in pair dissolution suggests probable similarity in pair formation: many females that left the area must have paired again, just as females that came to it paired again. (3) I made many observations of Prairie Warblers in southern Indiana, and much information about them was reported to me from localities near my study area. Breeding behavior, dates of breeding, and the general ecology of the species appeared homogeneous. (In connection with problems of reproductive success and other population dynamics, the question whether the study-area population was representative of some larger population is also critical. See Chapter 38 (esp. pp. 468–469) for additional evidence that the study area was typical of the surrounding region.)

If the pair bonds of birds that left the study area can be inferred from those of birds that came to it, as I hereafter assume, the problem presented by fragmentary individual histories is surmounted because territory histories will imply histories of individual birds. As one example, the half-histories of two females that spent, respectively, the first and second parts of the season on a study-area territory are statistically equal to a complete history of one female that changed breeding locations and mates.

I inspected 135 territories daily for a full season (1952–1966). Pair bonds were not location-specific; thus polygyny occurred on some sites in certain years and on different sites in others, as did the forms of monogamy. Territory sizes changed from year to year (Chapter 29). Therefore each year's data were independent; and I have counted a territory once for every year it was studied and occupied by at least one male that had at least one mate that laid one or more eggs. For territories occupied at the beginning of the season (defined p. 89) I disregarded later boundary fluctuations and compiled as many histories as there

were occupied sites. Unoccupied land that was taken over in midseason, other than through extension of an adjoining territory, was counted as a separate case with its own history. Territorial histories are also used in analysis of reproductive success (Chapter 33). That sample size differs from 135 because occasional events made a territory unsuitable for one analysis but not the other.

Except for second mates of polygynous males, which I sometimes did not find until a few days after they arrived and paired, I probably detected all individuals on the day they appeared. Arriving males were conspicuous, e.g. by singing, and the behavior of males near newly arrived females usually made females conspicuous too. When males or females disappeared from territories, this too was very quickly evident.

Determination of limits of season.—Central-tendency dates must be used in deciding whether some individuals were observed for a complete breeding season. The beginning of the season is the 22-day period defined on page 89. I examined about 50 newly paired females at that time, and none had incubation patches; it is probably safe to assume that bonds formed then were the first of the year. Such morphological evidence is lacking for males; but since the sex ratio during breeding was 1:1 (below, this chapter), a definition that is valid for females is probably valid for males.

The end of the season for the average individual is taken as 25 June, a date at which an estimated 40–50% of all females were incapable of further reproduction (p. 423). Application of this date to birds that disappeared in late June or early July will produce some errors, of course, but these should tend to cancel each other out.

“Midseason” is assigned a slightly different meaning for pair formation than for pair dissolution. Any pair formed at any date after the beginning of the season is considered formed in midseason. Any dissolution between the beginning of the season and 25 June was in midseason. The reason for this difference is that an average date must be used when birds left the area and could no longer be observed; but no cutoff date is needed when they came onto the area and the facts about them are known.

Discrimination between death and movement to new location.—I believe that midseason disappearances rarely were caused by death and have therefore treated unexplained disappearances as due to pair dissolution. Two females evidently died (feathers were scattered around two nests), but most females simply vanished immediately after failure of a nest that itself was usually undamaged (see Table 140, p. 408). Some females that vanished after nest failure I saw again later. Others disappeared just after fledglings left the nest (see case 3, p. 347), or they and the fledglings they were tending all disappeared (see p. 325), or they disappeared when young became independent. Each stage of fledgling development was associated with a change in parental behavior and sometimes was the occasion for the female’s leaving the male’s territory (p. 325 and Table 110). Again, some of these females were seen in later years.

Of males that disappeared in midseason, six were banded; three of these I saw in later years. Additional reasons for believing that male disappearances were not due to death are these facts: Nearly half the males that vanished had no mates (see p. 350), their females having disappeared earlier. Lack of a

mate was associated with relocations of territory, certainly at the beginning of the season (Chapter 5) and almost certainly thereafter (see the evidence on p. 344). Several males vanished while their females were incubating. Two were banded and seen later, and the behavior of others before disappearing suggested waning attachment to mates and territories (compare p. 429).

Number of banded birds.—Of 313 birds that formed sexual bonds on the 135 territories, 85 of 137 males and 119 of 176 females were color-banded; an individual is counted once for each year it supplied data. Continuities or discontinuities of behavior helped establish identity of unbanded birds, some of which also had distinguishing plumage or vocal characters. Very often the fact that individuals were unbanded could cause no error in classifying the sexual bond on a territory, e.g. when a banded male's banded female was replaced by an unbanded female.

HISTORIES OF TERRITORIES

Table 109 presents the 135 season-long territory histories. The primary subdivision is between sites on which polygyny did not occur (87%) and sites on which there was polygyny, however brief (13%). Within these two subsamples, territories are classed according to (1) duration of occupancy, (2) extent of turnover in occupants, (3) sex of individuals involved in turnover, and (4) sequence in which male and female disappeared, if both disappeared. Lines in the table are lettered and numbered for future reference.

The table is the basis for the next two sections and is discussed there.

DATES AND OTHER DETAILS OF MIDSEASON MOVEMENTS

Disappearance of males.—Sixteen males left territories before 25 June (11 prior to 16 June); none had been polygynous (Table 109: male never polygynous, I, B, 3 and 4; I, D). Extreme dates were 14 May and 23 June (mean 3 June; SD 15 days).

Seven of the males deserted incubating mates. Four of the deserted females then paired with males that took over the abandoned territories; 2 others incubated until their nests failed, then disappeared; the seventh disappeared 4 days after her mate, leaving half-incubated eggs.

Six males that disappeared were unmated, their females having disappeared previously. These males advertised before leaving themselves; the duration of unsuccessful advertising was 6, 7, 8, 14, 19, and 22 days. Three males disappeared at about the same time their mates did, after nests failed.

Reoccupation of territories by males.—Six territories that had been abandoned were taken over by new owners 3–11 days later (mean 7 days, SD 3 days). Three of these were unbanded and new to the study area; three were banded and were simultaneously holding other territories on the area. Extreme dates of reoccupation were 19 May and 1 July (mean 6 June, SD 19 days). All six reoccupying males gained mates.

Other midseason appearances by males.—Three males new to the study area settled on unoccupied land and acquired mates. A fourth, without abandoning his territory on the area, set up a second territory on unoccupied land and be-

TABLE 109
FORM AND STABILITY OF SEXUAL BONDS ON 135 TERRITORIES¹
DURING A FULL SEASON

Sexual bond(s) ²	Territories	
	N	% ⁴
Male never polygynous ³		
I. Occupied by pair, beginning of season.		
A. Occupied by same pair, 25 June		
1. Pair monogamous for season	61	45
2. Pair not monogamous for season		
a. Male at some time polygynous on second territory	3	2
b. Female paired again elsewhere after 25 June	2	1
B. Occupied by pair on 25 June but individual(s) changed		
1. Male unchanged, female replaced once	15	11
2. Male unchanged, female replaced twice	2	1
3. Female unchanged, male replaced once		
a. By male not engaged in polygyny	2	1
b. By male from second territory engaged in polygyny	2	1
4. Male and female both different		
a. Female of original pair disappeared before male	1	1
b. Male of original pair disappeared before female	1	1
C. Occupied only by male on 25 June		
1. Male unchanged, sole female disappeared	14	10
2. Male unchanged, 3 successive females disappeared	1	1
D. Unoccupied on 25 June		
1. Pair disappeared		
a. Female first	5	4
b. Male first	2	1
c. Simultaneously	3	2
II. Unoccupied, beginning of season		
A. Occupied on 25 June		
1. By pair formed in midseason		
a. Male not engaged in polygyny	2	1
b. Male engaged in polygyny on second territory	1	1
2. By male of pair formed and also dissolved in midseason	1	1
Male polygynous ³		
I. Occupied by 1 male and 2 females at beginning of season		
A. Occupied on 25 June		
1. By same individuals	1	1
2. By male and 1 original female	6	4
II. Occupied by pair, beginning of season		
A. Occupied on 25 June		
1. Male and female unchanged, 2 added females having paired with male successively and disappeared	2	1
2. Male and female unchanged, second female present	3	2
3. Male unchanged; second female present; original female having disappeared	2	1
4. Male unchanged, first female disappeared, replaced by 2 females	1	1
III. Occupied at beginning of season by male and 1 or 2 females, date of appearance of second female uncertain		
A. Occupied on 25 June by same male and 1 original female	2	1
Totals	135	100

¹ Methods are described on pages 348-349.

² Definitions of full season, beginning of season, midseason, and end of season are given on page 349.

³ Polygyny consists of having 2 females simultaneously, however briefly. Because the table classifies territories according to the bonds on them, territories of males that held 2 territories simultaneously but with only a single female on each are listed under "male never polygynous."

⁴ Percents as rounded do not total 100.

TABLE 110
CIRCUMSTANCES ASSOCIATED WITH DISAPPEARANCES¹ OF FEMALES
BEFORE 25 JUNE²

Stage of reproduction at disappearance	Sex bond of female			Totals
	Mated to monogamist ³	Mated to polygynist ⁴	Unmated	
Nest incomplete	2	0	0	2
Eggs under incubation	0	0	1	1
Nest had just failed	38 ⁴	11	2	51
Young had just left nest	3 ⁵	1	0	4
Young about 25 days old ³	2	0	0	2
Young just independent	0 ⁵	2	0	2
Totals	45	14	3	62

¹ Some disappearances are known, and all others are believed, not to have been caused by death; see pages 349–350.

² The significance of this date is discussed on page 349.

³ Young began to move around freely at this age; see Chapter 28.

⁴ Three females and their mates disappeared at about the same time.

⁵ Not shown is one case occurring after 25 June.

⁶ Males are classed as polygynists only if they had 2 females simultaneously on a single territory.

came polygynous. The four dates of occupation ranged between 22 May and 23 June (mean 6 June). Two additional cases are of considerable importance but are not reflected in Table 109 because the males, which took over land abandoned in midseason, did not gain females and therefore formed no bonds. These two males had been banded and had moved off the study area in earlier years. They advertised unsuccessfully for several days, then disappeared again. The significance of their cases is discussed below.

Discussion of male midseason movements.—Males gave up 16 territories before 25 June and acquired only 10. Four of the latter were occupied by birds that already had territories on the study area; thus the midseason loss of males (16) was greater than the gain (6); adj. Chi-square = 3.7; df = 1, $P \approx 0.05$. This raises the question whether the surrounding region was preferred to the study area. I believe such an interpretation is unwarranted and that two factors unrelated to preference account for the excess of emigrants: (1) From mid-June onward males passed out of breeding condition, the rate increasing with date. An individual might leave a territory while still capable of pairing but lose that capability before he acquired a new one. (2) Even if a male occupied a new territory, he would have to form a sexual bond before his case would be reflected in Table 109 and the data under discussion. The proportion of unmated females available at any one time was not great, and it too declined with date. Attracting a female was made more difficult by the existence of polygyny, since the sex ratio probably was 1:1 (below, this chapter). The cases (above) of the two banded males that took over evacuated territories in midseason but got no mates there indicate that acquiring a female was sometimes difficult. Similar instances involving unbanded males were fairly common; see the discussion on page 344. In sum, on a study area within a homogeneous region (therefore no part of it preferred over another by Prairie Warblers) emigrant males in midseason would probably always exceed immigrants that acquired both territories and mates.

Disappearance of females.—Sixty-two females disappeared before 25 June. Extreme dates were 11 May and 24 June (mean 9 June, SD 12 days). Table

TABLE 111
 FREQUENCY OF FEMALE DISAPPEARANCES AFTER NEST FAILURE,¹ ACCORDING
 TO NUMBER OF NESTS PREVIOUSLY BUILT² AND STAGE OF
 MOST RECENT NEST AT FAILURE

	Stage at failure					Totals
	Active building ³	Inactive building ³	Laying ⁴	Incubation ⁵	Nestling	
Nest 1						
Failures	5	17	41	72	18	153
Disappearances						
N	0	2	2	6	3	13
%	0	12	5	8	17	8
Nest 2						
Failures	2	5	12	52	15	86
Disappearances						
N	0	1	2	3	2	8
%	0	20	17	6	13	9
Nest 3						
Failures	1	0	15	24	4	44
Disappearances						
N	0	—	2	4	2	8
%	0	—	13	17	50	18
Totals						
Failures	8	22	68	148	37	283
Disappearances						
N	0	3	6	13	7	29
%	0	14	9	9	19	10

¹ Some disappearances are known, and all others are believed, not to have been caused by death; see pages 349–350. Nests that failed after 30 June are excluded; see text, this page.

² Females are those that paired on the study area at the beginning of the season.

³ See definitions on page 149.

⁴ The laying interval begins with laying of egg 1 and ends with laying of the final egg.

⁵ For this table, the incubation period begins with laying of the final egg and ends with hatching of the first egg to hatch.

110 summarizes the circumstances. At least 42 (68%) left territories on which they were the males' only mate; 14 (23%) left males with a second mate on the territory; 3 (5%) were unmated, having been deserted; and 3 (5%) left at about the same time as their monogamist males (and are tabulated in the monogamist column in Table 110).

Polygynous bonds involving one territory appeared no less stable than monogamous bonds. I tested whether females were more likely to leave a territory shared with another female than a territory on which the male had no second, concurrent mate. Territories from which there were more than one disappearance in a year were counted more than once. From sites on which the male had 2 mates, 15 of 37 females (41%) disappeared before 25 June. From sites on which the male had only one female, 43 to 46 of 101 females (43–46%) deserted their mates (3 females left approximately simultaneously with their males).

Pair-bond dissolution following nest failure probably was not associated either with number of nests built previously or with stage of reproduction at time of failure. Of the 62 females that disappeared, 51 (82%) did so within 1–2 days of nest failure (Table 110). Table 111 analyzes distribution of 29 disappearances following failure of first, second, and third nests at various stages; all failures

were prior to July. The table reveals no patterns except a tendency toward more frequent disappearance after third nests. This can be accounted for by date of failure. Most first-nest failures were in May, most second-nest failures prior to 15 June (never as late as 25 June); but third nests often failed after 25 June, when large numbers of females were no longer in breeding condition.

Arrival of females and formation of sexual bonds.—Thirty-six females moved to the study area and paired there in midseason (18 May–10 July; mean 14 June, SD 15 days); 7 left again before 25 June and therefore are also included among the 62 females that disappeared. Of the 36 arrivals, 24 paired with unmated males (mean 13 June, SD 16 days), 9 joined males on a territory on which there was already one female (mean 8 June, SD 16 days), and 3 paired with males that had a second territory elsewhere and a mate on that territory (mean 23 June). Clearly, date of midseason formation did not differ according to kind of sexual relationship formed; see the discussion of factors associated with the Prairie Warbler's polygyny (below). The mean interval between a monogamous male's loss of a female and acquisition of a replacement was about 8 days (SD 6 days) in 23 cases; included are 4 males that acquired territories, then mates, in midseason.

Using 62 and 36 for numbers of departures and arrivals (although 7 females fall in both categories), the exodus was greater than the influx; adj. Chi-square = 6.4; $df = 1$; $P \approx 0.01$. The explanation is probably like the one proposed for males. Further, possibly not all females that left mates were in condition to breed again immediately, which may have contributed to dissolution of their bonds (see p. 157). In any event, time was lost; even though females did not have to establish a territory and find a male that was unmated (because polygyny was an alternative), they had to choose among males or territories (see Verner 1964, Orians 1969). With every day that passed the number of available males dwindled, as they either reduced advertising to care for young and/or passed out of breeding condition. Some unmated females surely became incapable of pairing before they found a suitable male.

DESCRIPTIONS AND PROBABLE FREQUENCIES OF FORMS OF SEXUAL BOND

Forms of male bonds.—To describe the male side of the Prairie Warbler's mating system fully I have differentiated seven categories.

1. Season-long monogamy: No change of location involved.
2. Short-term monogamy: One mate for less than a full season. In all observed cases, the female was acquired at the beginning of the season and lost before 25 June; but occasional males probably do not acquire a mate until mid-season.
3. Successive monogamy without location change: Table 109 (male never polygynous: I, B, 1 and 2) shows many such cases.
4. Successive monogamy with location change: Some of the males that disappeared almost certainly settled elsewhere and paired again, as discussed on pages 345–346.
5. Polygyny on one territory: This commonest form of polygyny lasted various periods, sometimes all season. One polygynist may have had three mates simul-

taneously for a few days; all others had two. Sometimes one of two females disappeared and was replaced, reestablishing polygyny.

6. Polygyny on two territories: In all observed cases the second, concurrently held, territory was taken over in midseason.

7. Polygyny with location change: This category is hypothetical, but males that moved to new territories in midseason could have acquired two mates after moving; polygyny began at all dates (p. 363).

Forms of female bonds.—A female faithful to one male is monogamous, whether or not she shares him with another female; but the following system differentiates between sharing and nonsharing because of the potential biological importance of the distinction. To reduce complexity, the classification places less emphasis on location of the breeding site(s) than did the classification for males.

1. Season-long monogamy with a monogamous male.

2. Season-long monogamy with a polygynous male having one territory.

3. Season-long monogamy with a polygynous male having a mate on each of two territories.

4. Short-term monogamy with a monogamous male. An occasional female almost surely arrived from migration in midseason (see 5, below), and some bonds that dissolved in midseason must have been the females' only ones of season.

5. Short-term monogamy with a polygynous male: one case was observed; a late arrival (yearling, no incubation patch) joined a mated male for the rest of the season.

6. Successive monogamy with successively monogamous males: Some females moved from one monogamous male's territory to another's; the monogamous mate of some females disappeared and was replaced when a new male took over the territory (Table 109: male never polygynous, I, B, 3, a). Thus this category could be subdivided according to whether the female changed location.

7. Successive monogamy, one or more mates being polygynous: At least two sub-forms occurred: (a) a banded female moved from a monogamous male's territory and became the mate of a polygynist; (b) some females whose first, monogamous, mate disappeared remained on his territory and paired with a polygynist acquiring a second territory (Table 109: males never polygynous, I, B, 3, b). Some females probably paired with two polygynous males in succession, although I saw no definite case.

Male bonds during full season.—On the 135 territories whose histories were analyzed, 137 males formed the relationships shown in Table 112; 115 were present for a full season. Birds holding two territories simultaneously were counted only once, and an individual was tabulated each year he provided data.

The 22 (16%) males with incompletely known histories are shown only as having engaged in other than season-long monogamy, but enough is known about them to warrant an estimate of their activities over a full season: Six appeared in midseason and probably had already had territories elsewhere; thus they probably engaged either in successive monogamy with location change, or polygyny on two territories, or polygyny with location change. Sixteen disappeared in midseason, some probably not to acquire a new territory and mate, others very likely to pair again. The cases of these males were distributed among short-term monog-

TABLE 112
SEXUAL BONDS OF 137 MALES¹ DURING SINGLE BREEDING SEASONS

	Cases	
	N	%
Bond ² of males present full season ³		
Season-long monogamy	63	46
Successive monogamy without location change	17	12
Short-term monogamy	14	10
Polygyny on one territory		
Season-long	1	1
Until midseason	8	6
Beginning in midseason	8	6
Polygyny on two territories	4	3
Bond of males present less than full season ³		
Monogamy until midseason	16	12
Monogamy beginning in midseason	6	4
Totals	137	100

¹ These males bred on the 135 territories described on pages 348-349.

² Terms are defined on pages 354-355.

³ See definition on page 349.

amy, successive monogamy with location change, and polygyny with location change.

If the pair bonds of the 22 males are assumed to have been distributed in the same proportions as the bonds of males (except season-long monogamists) whose complete histories are known, frequencies of bonds for all 137 males (disregarding change or nonchange of location) were about as follows: season-long monogamy, 63 cases (46%); successive monogamy, 26 cases (19%); short-term monogamy, 23 cases (17%); polygyny, 25 cases (18%).

Male bonds on selected dates.—Analysis of relationships at representative dates may contribute to understanding the Prairie Warbler's polygyny. It will also be useful if the mating system of this population is to be compared with systems of other populations of Prairie Warblers or of other species, especially those in which bonds do not normally change during the season (as apparently in the Long-billed Marsh Wren; see Verner and Engelsen 1970: 558, but also 562).

Table 113, based on the 135 territorial histories, is a frequency distribution of mating status on 15 May, 1 June, 15 June, and 1 July. Note that territories were not tabulated on dates on which they were unoccupied. Since the data apply only to males on territory, the category "unmated" excludes unmated nonterritorial individuals. The proportion of unmated males of this latter sort can be estimated using the fact that 131 males formed bonds at the beginning of the season on the 135 territories (Table 109): If the potential male breeding population is taken to be 131, the difference between 131 and total number of territory holders on any date (Table 113) suggests the number of nonterritorial males. (As discussed above and in Chapter 38, probably very few adults died during the breeding season). Results are discussed below.

1. The percentage of unmated territorial males, 0 in mid-May, had climbed to about 6% by 1 June and 18% by 1 July. Meanwhile the number of males

TABLE 113
NUMBERS OF POLYGYNOUS, MONOGAMOUS, AND UNMATED TERRITORIAL
MALES AT VARIOUS DATES¹

Dates	Marital status of males						Total males on territory
	Polygynous		Monogamous		Unmated ²		
	N	%	N	%	N	%	
15 May	6	5	120	95	0	0	126
1 June	13	10	108	84	8	6	129
15 June	11	9	98	78	17	13	126
1 July	4	4	90	79	20	18	114

¹ The males were those on the 135 territories described on pages 348-349.

² The table does not show nonterritorial males; therefore the category "unmated" does not necessarily include all unmated males in the population; see page 356.

on territory was nearly constant until 15 June, then dropped rather sharply. These data indicate that after losing mates males tended to remain and advertise until about 15 June and then either to seek new territories or to become non-territorial for the year.

2. Monogamous male numbers fell from a peak (95%) on 15 May to 84% on 1 June, then declined little until 1 July. But the stability of numbers in June conceals important changes for individuals: For example, in the second half of June, 17 monogamous males lost mates; 14 of those males disappeared, while 3 advertised without success. However, recruitment to the monogamous group partly offset these changes; 7 polygynists lost 1 female, and 2 newly arrived males took over vacant territories and paired.

3. Only 5% of territorial males had 2 females on 15 May (see Verner and Willson 1969: 6), but by 1 June 10% had 2 females. This proportion continued until many females quit breeding. The greater frequency of polygyny in midseason is discussed on page 363.

Female bonds during full season.—Among the 176 females that nested on the 135 territories, Table 114 distinguishes between 85 (48%) whose full histories are known and 91 (52%) that were present for less than a season. Most birds (61) in the former category engaged in season-long monogamy with a monogamous male. The rest spent the period in season-long monogamy with a polygynous male having one (14 cases) or two (3 cases) territories, or in some form of successive relationships (6), or in short-term monogamy with a polygynous male (1).

Most of the complexity of the mating system was attributable to the 91 females present only a fraction of the season. Table 114 shows that while on the area 70 were mated to monogamists, 21 to polygynists. Because of the size and importance of this group, it is desirable to estimate their bonds during that part of the season in which they were not present. I have therefore assumed that bonds formed off the area by females that left in midseason were distributed at the same frequencies as bonds formed on the area by females that arrived in midseason (see p. 348). Similarly, bonds of birds that were present only in the first part of the season have been used in estimating the early-season bonds of females present only from midseason onward. (To reduce complexity the seven females that arrived after the beginning of the season and disappeared before its

TABLE 114
SEXUAL BONDS OF 176¹ FEMALES DURING SINGLE BREEDING SEASONS

Form of bond ²	Females	
	N	% ⁴
Females present full season ³		
Season-long monogamy		
With monogamous male	61	35
With polygynous male		
One territory	14	8
Two territories	3	2
Short-term monogamy		
With polygynous male	1	1
Successive monogamy		
With successively monogamous males	3	2
One or more males polygynous	3	2
Females present less than full season		
Monogamy with monogamous male		
Until midseason	45	26
Beginning midseason		
Ending midseason	4	2
Lasting till end of season	21	12
Monogamy with polygynous male		
Until midseason	10	6
Beginning midseason		
Ending midseason	3	2
Lasting till end of season	8	5
Totals	176	100

¹ These females bred on the 135 territories described on pages 348-349.

² Terms are defined on pages 354-355. Only bonds formed on the study area are included.

³ A full season is defined on page 349. The female shown as short-term monogamous was not present at the beginning of the season but had not bred before she came to the study area; see pages 348, 355.

⁴ Percents as rounded do not total 100.

end were treated as late arrivals only.) The partial histories obtained by these assumptions I have combined with their complementary observed partial histories and have thus obtained estimates of full-season relationships. One example of the method will be given.

Ten of 55 females that left in midseason had been paired to polygynists, 45 to monogamists. Probably only about 36 (65%) of these females paired again, an estimate based on the ratio of midseason disappearances to arrivals (p. 346). Assuming that whether a female paired again was not associated with the form of her earlier bond, 16 females that had engaged in short-term monogamy with a monogamous male and 3 whose bond had been short-term monogamy with a polygynous male failed to pair after leaving the area. Of the 36 that I assumed did pair again after leaving the area, some must have joined unmated males that had been monogamists but had lost mates; others must have joined mated males and made them polygynists. The proportions selecting those alternatives can be estimated from the fact that 25 females arriving on the study area in midseason joined males in monogamy and 11 in polygyny (Table 114); it is a coincidence that the 25:11 ratio can be applied as absolute numbers to the 36 females that left the area. If the bond formed elsewhere was independent of the bond on the study area, 2 of the 11 females hypothetically mating with polygynists off the

TABLE 115
SEX RATIO OF PRAIRIE WARBLERS BREEDING ON STUDY AREA,¹
ACCORDING TO DATE

	Number of breeding individuals per date				
	Beginning of season ²	15 May	1 June	15 June	1 July
Males	131	126	128	126	114
Females	138-140	132	134	120	111
Females per male ³	1.05-1.07	1.05	1.05	0.95	0.97

¹ Data were obtained on the 135 territories described on pages 348-349. Only individuals that formed sexual bonds on the study area were counted; e.g. see page 352.

² See definition, pages 89, 349.

³ It was uncertain whether 2 males became polygynous at the beginning of the season or soon thereafter.

area exchanged 1 polygynist for another; 9 had previously been mated to monogamists. Of the 25 females assumed to have paired with monogamists after leaving the area, 5 had deserted polygynists, the rest monogamists. Thus, 20 of the 36 females under consideration probably engaged in successive monogamy with successively monogamous males, and 16 probably took part in successive monogamy, one or more males being polygynous.

Combining the completely known and the calculated histories, estimated relationships of all 176 females were as follows: season-long monogamy with a monogamous male, 61 cases (35%); season-long monogamy with a polygynous male, 17 (10%); short-term monogamy with a monogamous male, 18 (10%); short-term monogamy with a polygynous male, 4 (2%); successive monogamy with successively monogamous males, 42 (24%); successive monogamy, one or more males being polygynous, 34 (19%). None of the 91 females present for less than a season was assumed to have paired with more than 2 males during a year, but occasional individuals probably did have 3 mates (see p. 346).

Female bonds on selected dates.—Seven (possibly 9) of 131 territories occupied at the beginning of the season were held by males polygynous at that time (Table 109). Thus 138-140 females formed the breeding population at the beginning of the season. If 138 is taken as 100%, percentages of females that were unmated at subsequent dates can be estimated (compare p. 356).

Table 115 shows that numbers of breeding females were 132 on 15 May, 134 on 1 June, 120 on 15 June, and 111 on 1 July. Thus, until early June few females were unmated at any one time, but by mid-June about 13% were unmated. On 16 June occasional females probably had recently passed out of breeding condition. Another factor in the decline of mated females may be the fact that finding new mates after pair dissolution doubtless took longer in mid-June than earlier, because by the later date more males were caring for young and had reduced advertising (see Chapters 8 and 25). If obtaining a male did take longer, the number of females engaged in bonds at any one time would decrease.

By 1 July, 20% of females were no longer on breeding territories, compared to 13% of males (see Table 115). Most females probably were no longer capable of breeding (see Chapter 34).

Number of mates per individual per season.—The 115 males observed for a season had the following numbers of mates: 1 mate, 77 males (67%); 2 mates, 31 (27%); 3 mates, 6 (5%); 4 mates, 1 (1%). The proportion of one-mate males is overestimated in these figures, which exclude the 22 males present only part of the season. When these 22 are added and assigned the bonds proposed on page 356, percentages are approximately as follows: 1 mate, 63%; 2 mates, 29%; 3 mates, 7%; 4 mates, 1%.

Among the 85 females observed for a season, 79 (93%) had 1 mate and 6 had 2. If the bonds of the 91 females present only part of the season were about as proposed above, 100 females (57%) had 1 mate and 76 (43%) had 2 or more.

SEX RATIO

Sex ratio is no longer generally believed to dictate a species' mating system (see Selander 1965, Verner and Willson 1966; but see Wiley 1974), but the sex ratio of the Prairie Warbler will be examined before further consideration of its polygyny. Nothing is known of primary and secondary ratios (Mayr 1939).

Methods for birds less than 1 year old.—Beginning in 1958, when I could sex almost all young of the year observed in the field (see Nolan and Mumford 1965: 323, 324; see Chapter 41 and Appendix 5), I recorded the sex of all independent immatures that I found. Those detected because they had called or sung were ignored in the following analysis, to avoid bias in favor of males. I also recorded perching and foraging heights of most individuals, doing so once per minute for those watched several minutes.

I gathered data on sex ratio from museum specimens, tabulating sex of skins killed on dates when male Prairie Warblers generally do not display visibly or audibly. Included were two groups:

1. Birds killed 1 July–31 October in the United States and Canada and now in the collections of Royal Ontario Museum, Smithsonian Institution, Academy of Natural Sciences of Philadelphia, Chicago Natural History Museum, Carnegie Museum, Cleveland Museum, American Museum of Natural History, Museum of Comparative Zoology of Harvard University, Museum of Zoology of University of Michigan; and the museums of the University of Florida, Cornell University, Ohio State University, Purdue University, and University of Kansas.

2. Specimens taken 1 August–31 May outside the United States and in the collections of the foregoing institutions and of the Museum of Vertebrate Zoology of the University of California and the Peabody Museum of Natural History of Yale University. Dr. J. D. MacDonald generously provided sex and age data on 40 specimens that were examined by workers at the British Museum (Natural History).

Where I disagreed with a museum label I relied on my own judgment of age and also of sex unless there was indication that the gonads had been examined.

Clearly, these museum data must be viewed with caution. Even if samples were unbiased by behavior that would make one sex more conspicuous (see p. 362), pooling cases from the entire range and from over 100 years assumes uniformity in space and time, for which there is no evidence. Further, data will be reliable only if Prairie Warblers do not partition out the habitat according

to sex-age classes, or if collectors collected representatively in all habitats. Age- or sex-specific geographical or habitat differences, especially in the winter range, are very possible.

Methods for birds of breeding age.—Counts of breeding birds on 135 territories (p. 348, Table 115) provide sex ratios. Because I included only males that held territories and obtained mates but counted all females, data are slightly biased in favor of females (probably two–four individuals) on all dates.

I compared the total days during which polygynous males on the 135 territories had two mates with the total days during which unmated males had no mates, between 20 May (about when pair dissolution began) and 25 June (see p. 349). An approximate balance between “polygyny-days” and “unmated-days” would imply that for every polygynous male another male had no female. Because dates of appearance of a few second females were estimated (p. 349), the total of polygyny-days is approximate. Unmated-days were counted beginning with disappearance of a monogamous male’s mate and ending with her replacement by a new female, or 25 June, or the male’s disappearance, whichever was earliest.

I recorded all sightings and heights of adult males and females seen after 15 July (1952–1962), excluding individuals discovered because they called or sang and individuals still nesting and/or feeding young. (Prairie Warblers of both sexes occupied the same habitat after the breeding season as during it; I established this by persistent late-summer searches of habitats surrounding the study area. See also Chapter 2.)

Two museum samples were selected, comparable to those described on page 360 except that the start of the period for the breeding-range sample was 16 July; prior to that date most males could have been noticed and collected because they sang.

Treatment of data on known migrants.—It is clear that sex-age classes of Prairie Warblers killed in migration through Leon County, Florida were not representative of the species’ sex ratio (Chapters 3 and 36). Therefore I ignored all samples of known migrants in the following analysis.

Results: Birds less than 1 year old.—Samples selected by different methods and at somewhat different ages consistently reveal a balanced sex ratio between independence and beginning of spring migration. On the study area (1958–1962), 23 independent young males and 25 independent young females were seen. Museum skins of immature males from the United States and Canada numbered 134, of immature females 124. Winter-range specimens of young males numbered 139, of females 141. If these last totals were reduced by excluding 12 specimens from April, 1 from May, and 11 from unknown dates (because males migrate earlier and the population exposed to collection after March is biased toward females), winter-range totals would be 132 males and 124 females.

Results: Birds of breeding age.—The breeding sex ratio on the study area was balanced; an apparent imbalance in favor of males outside the breeding season is believed attributable to behavioral differences.

At the beginning of the season 131 males and 138–140 females were present on 135 territories (Table 115); methodological bias toward females could account for the difference, which is not significant ($P > 0.5$). The ratio continued to favor females, but subject to the same bias, until sometime in the first half of

June, after which males predominated slightly. The total of polygyny days was about 467, as compared to 446 unmated-days ($P \cong 0.5$).

Adult male sightings on the study area in the postbreeding period number 198, adult female 139 ($P < 0.005$); this ratio is 1.0:0.7. Adult male specimens collected after 15 July in the United States number 37, adult female 26, also a ratio of 1.0:0.7. Adult male winter-range specimens number 193 and adult female 91, a ratio of 1.0:0.5.

In considering the differences among these data, it is important that the postbreeding ratio on the study area was identical with that for birds collected in the same period in the rest of the breeding range; thus the study-area population presents no special problem. Two explanations seem possible: (1) Males may outnumber females. A ratio at unity during breeding but favoring males at other times could point to a floating surplus of nonterritorial males during reproduction (see Watson and Jenkins 1968 and bibliography therein; Hickey 1940, Stewart and Aldrich 1951, Hensley and Cope 1951, Tompa 1964, Krebs 1971). Any such surplus males might conceivably escape observation by an investigator on breeding territories; after breeding they might be detected because then they could move about freely and conspicuously. (2) The ratio may be balanced. Close daily study of a breeding population should lead the investigator to know the whereabouts of almost all individuals and to estimate the sex ratio accurately; during the nonbreeding period behavioral differences (other than vocal behavior) might make males more conspicuous than females. The merits of these two possibilities will be considered.

Nothing suggested the existence of nonterritorial males on or seeking access to my area. The evidence indicates the contrary: Space for more territories always appeared available, its location varying from year to year. Note that even at the beginning of the season only 131 of 135 territories were occupied. When males disappeared and were replaced, it was after a mean 7 days during which their territories stood vacant (p. 350). More significant still, some were not replaced. Thus it is unlikely that males outnumbered females or that any males were excluded from breeding (compare p. 16).

In the field I was conscious of no nonvocal behavior that might cause males to be more conspicuous, but subsequent analysis of heights at which I observed the sexes reveals a difference. As described in Chapter 39, the median height recorded for adult males between the end of breeding and migration was significantly ($P \cong 0.01$) greater than that for adult females. Further, adult males were seen above 3 m on 159 (33%) of 480 recorded sightings, females on 71 (24%) of 296 recorded sightings; adj. Chi-square = 6.9; $df = 1$; $P < 0.01$. High birds may be easier to see, or movement to a high perch may attract attention; either possibility could explain the greater frequency of male postbreeding records, at least on the study area. Support for this suggestion is that immature males and immature females, seen in equal numbers, were observed at identical heights (see pp. 492–493); nor did number of observations of immatures above 3 m differ according to sex.

To sum up, for familiar theoretical reasons (see, e.g. Williams 1966: 146–157), the foregoing evidence of a 1:1 sex ratio in newly independent Prairie Warblers is expected. If that ratio continued to the beginning of spring migration, as the museum data suggest, a skewed ratio later in life would require both a complex

explanation for the breeding season data and differential mortality during breeding, neither of which is suggested by evidence (see Chapter 38). Therefore the imbalance after breeding is probably the product of behavioral differences (compare Roberts' 1971: 166 similar explanation of a 2:1 capture ratio in favor of male Yellow Warblers over females).

FACTORS ASSOCIATED WITH POLYGyny

Polygyny is infrequent among North American passerines (Verner and Willson 1969; see also Lack 1968: 148–153), and the Prairie Warbler's habitat is somewhat different from that of other polygynous perching birds (Verner and Willson 1966). Therefore its mating system is of considerable interest. According to current theory (summarized by Orians 1969), the central problem in the evolution of avian polygyny is to analyze the advantages that will compensate females for the losses suffered because of electing to pair with already mated males. Such females necessarily get only part of the attention of the male. They also face the prospect that their young will receive less than full paternal care. Further, the presence of more than one female and brood on a territory may have disadvantageous density effects. The rest of the chapter summarizes information relevant to this problem in the Prairie Warbler.

Date.—Polygynous bonds formed throughout the breeding season (once on 10 July); mean dates of midseason formation of monogamous and polygynous bonds were about the same (p. 354). The proportion of females that selected already mated males changed from 5–6% at the beginning of the season (7–9 of 138–140 females) to 27% at midseason (9 of 33 females, counting only mates of males with one territory). However, it must have been much easier for females to find unmated males at the beginning of the season; by 1 June only 6% of territorial males were unmated (Table 113), which might cause females seeking a male to be less selective or to search less persistently for an unmated bird (see below). It may be less noteworthy that polygyny increased during the summer than that 73% of bonds formed in midseason were monogamous, considering that unmated males were a small minority. This seems to point to a female preference for monogamists and reiterate the question why any selected mated males.

Status of males on nearby territories.—The theory that females will prefer already mated males if chances of reproductive success are enhanced by pairing with them predicts that under appropriate conditions polygynous bonds will form even though unmated males are available (Orians 1969). Such cases occurred throughout the season; at least six males obtained second mates despite the presence nearby of unmated advertising males. Three times an unmated male and the male that obtained a second mate had adjoining territories; one male remained unmated from 31 May until the end of the season, while two polygynous bonds formed next to him. As many as seven other cases of polygyny may have originated when unmated males were present on the area.

Stage of reproduction of first female when second female appeared.—Among 13 cases (including those of males with two territories), the stage of reproduction of the first female when the second bond formed was as follows: pre-nest-building,

TABLE 116
ANALYSIS OF COVARIANCE OF REGRESSION OF DURATION OF PRE-PAIR-
FORMATION PERIOD ON RELATIVE DATE OF ARRIVAL¹ OF
13 POLYGYNOUS AND 85 MONOGAMOUS MALES

Source of variation	Sums of squares and cross products			Deviations about regression			
	xx	xy	yy	$yy - (xy)^2/x^2$	df	ms	F
Between samples	13.453	-9.229	6.331				
Within samples	1401.169	-560.138	2020.771	1796.848	97	18.524	
Total	1414.622	-569.367	2027.102	1898.646	96		
Difference for testing among adjusted sample means				101.798	1	101.798	5.50

¹ Details are described on pages 364-365.

3 cases; nest building, 1; egg-laying, 1; incubation, 8. Concentration of cases in the incubation period suggests that second bonds tended to form when males' attention was not focused on the activity of a mate or, especially, on parental duties; note, however, that incubation, as the longest stage prior to nest-leaving, would have most cases even if the distribution were random. The three instances during the pre-nest-building period all occurred at the beginning of the season, when that period was sometimes prolonged, i.e. even in these cases the polygynists formed their two bonds asynchronously, the second when there was a lull in the demands of the first relationship.

Territories of polygynous males.—As shown in Tables 106 and 107 and discussed in Chapter 29, maximum and utilized territories of polygynists averaged significantly larger than those of monogamists. The difference is based on polygynists with one territory and would be greater still if data from males with two territories were included. Other evidence in Chapter 29 also points to territory size as an important factor in male success in obtaining and keeping mates (compare Schoener 1968: 132). Three among the few reported cases of casual polygyny by other parulids were associated with peculiarities in shape or size of territory (see Stewart 1953, Mayfield 1960: 57, Welsh 1971).

As described in Chapter 29, vegetational differences between territories of polygynous and monogamous males were not detected.

Age of polygynous males.—It is not clear whether polygynists tended to be older. Nine had been banded as adults in prior years, and 2 of these were polygynous in 2 successive years. Three other polygynists were unbanded, and their territories had been held in the preceding year by males that had not returned; most such new occupants of territories were surely yearlings (see p. 22), but some were old males that had relocated to new territories. Knowledge that 9 of 12 polygynous birds were old is inconclusive in a population in which 65% of all breeding males were older than one year (Chapter 38). Indirect evidence that polygyny was more frequent among old males are the facts that polygynous males held significantly larger territories and that territories of old males were significantly larger than those of yearlings (see Chapter 29).

Duration of pre-pair-formation period of polygynous and monogamous males.—If a polygynous male or his territory is sufficiently attractive to his second female

TABLE 117
REPRODUCTIVE EFFORT AND PRODUCTION OF FLEDGLINGS ON 104 TERRITORIES,
ACCORDING TO FORM OF SEXUAL BOND ON TERRITORY

Form of bond ¹	Reproductive effort											
	Nests built ²			Eggs laid ³			Eggs hatched ⁴			Fledglings produced ⁵		
	Median	Mean	SD	Median	Mean	SD	Median	Mean	SD	Median	Mean	SD
Polygyny (N = 16)	3.8	4.2	1.8	13.5	14.6	6.3	6.5	6.5	2.3	3.0	3.0	2.3
Season-long monogamy (N = 48)	3.3	3.4	1.2	11.0	11.5	4.4	4.1	4.5	2.1	2.7	2.3	1.8
Successive monogamy (N = 19)	2.8	2.9	0.9	10.0	9.7	2.6	3.1	2.8	1.8	0.5	1.5	1.6
Short-term monogamy (N = 21)	1.0	1.7	0.8	4.0	6.1	3.0	0.5	1.6	1.8	0.2	0.5	1.2

¹ See text for definitions and details.

² Distributions, according to forms of bond, follow: Among polygynists, on 2 territories nests built numbered 2; on 5 territories 3; on 3 territories 4; on 3 territories 5; on 2 territories 6; on 1 territory 9. Among season-long monogamists, on 2 territories nests built numbered 1; on 8 territories 2; on 18 territories 3; on 13 territories 4; on 5 territories 5; on 1 territory 6; on 1 territory 7. Among successive monogamists, on 7 territories nests built numbered 2; on 8 territories 3; on 3 territories 4; on 1 territory 5. Among short-term monogamists, on 11 territories nests built numbered 1; on 6 territories 2; on 4 territories 3.

³ See page 366 for methods. Distributions, according to bond, follow: Among polygynists, on 1 territory eggs laid numbered 1; on 2 territories 8; on 3 territories 10; on 1 territory 12; on 1 territory 13; on 1 territory 14; on 1 territory 15; on 1 territory 16; on 1 territory 18; on 1 territory 19; on 1 territory 21; on 1 territory 24; on 1 territory 29. Among season-long monogamists, on 2 territories eggs laid numbered 4; on 1 territory 5; on 2 territories 7; on 6 territories 8; on 4 territories 9; on 5 territories 10; on 8 territories 11; on 4 territories 12; on 3 territories 13; on 6 territories 15; on 2 territories 16; on 2 territories 17; on 1 territory 18; on 1 territory 19; on 1 territory 21. Among successive monogamists, on 1 territory eggs laid numbered 6; on 4 territories 7; on 2 territories 8; on 2 territories 9; on 1 territory 10; on 7 territories 11; on 1 territory 14; on 1 territory 16. Among short-term monogamists, on 1 territory eggs laid numbered 2; on 1 territory 3; on 9 territories 4; on 2 territories 6; on 1 territory 7; on 3 territories 8; on 1 territory 9; on 1 territory 10; on 1 territory 12; on 1 territory 13.

⁴ See page 366 for methods. Distribution can be sufficiently inferred from footnote 3.

⁵ A fledgling is a young bird (excluding cowbirds) that left the nest. Distribution, according to bond, follows: Among polygynists, on 4 territories fledglings produced numbered 0; on 2 territories 2; on 4 territories 3; on 3 territories 4; on 1 territory 6; on 2 territories 7. Among season-long monogamists, on 15 territories fledglings produced numbered 0; on 7 territories 2; on 11 territories 3; on 12 territories 4; on 2 territories 5; on 1 territory 7. Among successive monogamists, on 10 territories fledglings produced numbered 0; on 1 territory 2; on 6 territories 3; on 2 territories 4. Among short-term monogamists, on 17 territories fledglings produced numbered 0; on 1 territory 1; on 2 territories 2; on 1 territory 3.

to outweigh any disadvantage to her of sharing her mate, that attraction should have at least equal effect on his first female (compare Verner 1964). My hypothesis that males destined to become polygynous might have to wait a shorter time for first mates than monogamists waited for their only mates proved to be supported by evidence: I compared pre-pair-formation periods of 13 polygynists and 85 monogamists, analyzing covariance of the regression of length of this period on relative date of arrival (Table 116; see p. 91). In a test for homogeneity of regression coefficients, the F -ratio is 0.448, and I conclude that the lines are parallel. In the test of whether the adjusted means differ, $F = 5.495$; $df = 1$ and 97 ; $P < 0.05$. The mean pre-pair-formation period of polygynists was 6.6 days (SD 4.8 days), of monogamists 7.4 days (SD 4.7 days). Corrected to a single X -value, the adjusted mean for the period of polygynists is 6.2 days and for monogamists 7.4 days.

Annual variation in spring weather and therefore in pre-pair-formation periods could have affected this comparison, in view of the small size of the sample of

TABLE 118
FEMALE-DAYS ATTEMPTING TO PRODUCE FLEDGLINGS,^{1,2} ACCORDING TO
FORM OF SEXUAL BOND ON THE TERRITORY

Female-days	Form of sexual bond			
	Polygyny ³ (N = 14)	Season-long monogamy ⁴ (N = 48)	Successive monogamy ⁵ (N = 18)	Short-term monogamy ⁶ (N = 21)
Mean	98.6	69.1	62.0	32.3
Extremes	80-155	35-86	43-84	13-51
SD	21.3	11.9	14.0	13.2

¹ See definition, text, this page.

² A fledgling is a young bird that left the nest at the end of a normal nestling interval.

³ See pages 334-336 for further details; see also page 349.

⁴ Only pairs that remained together until at least 25 June are included.

⁵ This group includes territories on which one pair dissolved (male, female, or both leaving) and was succeeded by a second pair.

⁶ This group includes territories on which only one pair was present and for less than a full season (see page 349).

polygynists. Nevertheless, the data are evidence that polygynous males (while still unmated) and/or their territories were more attractive to females.

Male productivity.—Table 117 presents statistics on numbers of nests built, eggs laid, eggs hatched, and fledglings produced on 104 territories, according to whether polygyny or a form of monogamy was the pair bond. (Methods are described in connection with sample 2, p. 397.) With a single exception these territories were held by only one male during the season, and the territorial data are therefore estimates of the reproductive consequences to the individual male of the form of bond he was able to establish. As expected, the effort and success of the combined mates of polygynists were greater by every measure than those of the monogamists pooled. Within the monogamist group, a gradient extends uniformly from season-long, the most productive form, through successive to short-term, the least productive. Applying a Kruskal-Wallis analysis of variance by ranks to each of the 4 measures of reproductive effort and success according to form of pair bond, *H* is significant beyond the 0.001 point; in parametric analyses (not shown), *F* is significant at 99%. Considering only Prairie Warbler fledglings produced and comparing polygynists against the three forms of monogamists pooled (Mann-Whitney U Test), *z* = 1.90; *P* one-tailed = 0.029. On the other hand, the difference between polygynists and season-long monogamists is nonsignificant.

The foregoing reproductive differences according to bond may ultimately be traceable to factors such as age and qualitative differences in males or their territories, but the differences can be superficially accounted for simply by variation in the amount of time females spent attempting to reproduce in the different forms of pair bond. Using the concept "female-days attempting to produce fledglings" for each territory about which I had the information, I counted the days, inclusive, between the day each female joined her mate and the day her last nest there failed or produced fledglings. When more than one female bred on the territory, days spent by all were summed. Table 118 shows that female-days attempting to produce fledglings were greatest where there was polygyny and decreased through the forms of monogamy in the same order as the order of productivity. In an analysis of variance (not shown) *F* is significant at 99%.

TABLE 119
NEST SUCCESS ON TERRITORIES OF MONOGAMOUS AND POLYGYNOUS MALES¹

Number of young leaving nest	Nests on territories of monogamists (N = 88)		Nests on territories of polygynists (N = 16)	
	N	%	N	% ²
0	203	81	51	76
1	3	1	0	0
2	8	3	5	7
3	20	8	6	9
4	16	6	5	7
5	2	1	0	0
Totals	252	100	67	100
Mean/successful nest	3.1		3.0	
SD	0.9		0.8	

¹ See text, this page, for description of samples.

² Percents as rounded do not total 100.

Interestingly, the mean number of days attempting to produce fledglings on territories where there was season-long monogamy (69.1 days; SD 11.9 days) was greater ($P \cong 0.05$) than the mean number (59.9 days; SD 31.0 days) for the pooled territories on which the 3 other bonds prevailed. This result is expected, because the sex ratio was almost surely balanced (above): The fact that the polygynists among the pooled group had more than one female for varying periods could not possibly compensate for (1) reproductive time lost by other males as a result of midseason moves of females, not all of which paired again, and (2) time during which some males had no mate because polygynists had two. The greater female time spent breeding on territories of season-long monogamists is part of the explanation for the different trends in productiveness shown in Tables 143 and 144 (see pp. 417–419).

Female productivity.—Because a representative sample of season-long histories of individual females cannot be obtained (see p. 347), productivity of females that did and did not share their males cannot be compared directly. However, nest success on territories classified according to form of pair bond can be compared, as can brood size in successful nests on those territories. Production of cowbirds is ignored in both analyses.

Table 119 is based on 88 territories of monogamists and 16 on which males were polygynous at least part of the time. All nests of the season are included; some were built when polygynists had only one mate, but this should not affect the comparison. As is apparent, statistical evidence suggests no greater productivity on territories where there was polygyny, even when these are compared with territories where the reproductive effort was least persistent, i.e. territories of males that were short-term and/or successive monogamists.

Data not shown in Table 119 deserve mention: On territories of polygynists, 6 of 21 (29%) first nests succeeded, as against only 13 of 88 (15%) on territories of monogamists. This difference, though not significant, may be of special interest because the comparison is between nests built at roughly the same dates and fledglings from early nests may have a greater chance of surviving to reproductive age (see pp. 398–399).

Evidence of importance of male in parental care.—Monogamous males made 45.5% of all feeding trips to nestlings (p. 261). Rather clearly, no unassisted female could both warm and feed a brood through several days of cold wet weather, a condition not uncommon in May. The female's need for male help in such circumstances is suggested by my observations of her reliance on him in another adverse situation, when her nest was exposed to direct sun and she could not leave nestlings unsheltered (see pp. 263–264).

Circumstantial evidence of the importance of male care is that his singing decreased greatly and sharply after his eggs hatched (Chapters 8 and 25); no polygynous bond was formed thereafter. The male thus traded the chance to acquire a second female for the evidently more profitable job of protecting his investment in young that were nearing the age of nest-leaving (compare Trivers 1972). If this strategy improved his own fitness, the importance of the male's contribution to female reproductive success cannot be doubted.

One adult probably could usually raise only three fledglings to independence (p. 321); yet four was a frequent brood size at nest-leaving (Table 142). Again, the importance of the male is obvious. The further fact that monogamous males tended fledglings at the expense of full-scale advertising may suggest that even though fewer than four young could be brought to independence by the female alone they were less likely to reach reproductive age.

The foregoing has emphasized feeding and brooding young. Males also performed distraction display, which presumably is more effective when performed by two parents than by one.

Parental behavior of polygynous males.—No polygynous male had two broods at the same stage simultaneously. This was the result of heavy nest predation and the forming of pairs throughout the season rather than of any behavioral mechanism reducing in-phase nesting by two mates (compare Verner 1963). Only two polygynous males had simultaneously dependent broods produced by different mates, and the older offspring were largely or entirely able to care for themselves by the time the eggs of the younger broods hatched. During brief periods, at least, the males fed both sets of young, appearing to be normally attentive to the nestlings (see p. 267). Thus, as mentioned on page 267, observed situations of polygynous males with two families were not much different from situations of monogamous males with two broods by one mate. In fact, offspring of polygynists were cared for by both their parents, whereas first broods of monogamists lost the attention of their mother when she began to incubate again.

In sum, while the importance of the male's parental contribution is clear, conditions on the study area were such that mates of polygynists hardly ever confronted a situation in which they might suffer disadvantage. If this is common in Prairie Warbler populations, a constraint believed to work against the evolution of polygyny in passerines is of much reduced importance in this species.

Extent of aggressive behavior between mates of polygynists.—Intrasexual aggression by females promotes monogamy (see Hinde 1956: 355) or partitioning of subterritories among mates of polygynists (see Orians 1961: 294). In view of the relationship of female aggressiveness to mating system, aggressive behavior in female Prairie Warblers is treated at this point.

Except in melees, when the participants perhaps could not discriminate between the sexes because of rapid action (p. 50), occasional encounters near the nest (Chapter 22), and the aftermath of sexual chases, female aggressiveness was very rare. It usually consisted of no more than brief tense crouching and was directed at other females that approached too closely. However, I saw two fights as long and intense as those between very aggressive males, and one was between mates of a polygynist. Conceivably the other fight prevented polygyny from occurring; it took place near a nest and is described in connection with nest defense (see p. 225).

The fight between mates of the same male occurred as follows: On the day after the nest of female B failed, female A's three nestlings were 6 days old; the male was alternately carrying food to these and watching female B as she searched for a new nest site. I suddenly noticed both females near the male, which was carrying food. The two flew at each other, rose 1–2 m in a flutter-up and descended together to the ground. The male started to fly toward the nest with the food, but one female pursued him and drove him to the ground. Then began a 10-min fight between the females (flutter-ups with kicking; slow pursuits in undulating flight and low-intensity butterfly flight; perching 3–4 m apart in tense crouch, wings out, head forward). The fight covered a considerable area, and the females appeared equally aggressive. Occasionally when one perched and appeared ready to quit, the other turned, flew past the perching bird, and elicited pursuit (compare p. 39). I lost sight of the females when they moved to a different part of the territory, still fighting. Shortly afterward female A was brooding.

In contrast, among many instances in which females were unaggressive toward others are three episodes in which mates of polygynists showed great tolerance toward each other. Probably the same individuals (unbanded) were involved in two of the cases, which are described on page 225. The third episode was as follows: On 10 May, banded female B arrived and joined a male during the pre-nest-building period of his mate female A. Female B was courted vigorously by this male and his two neighbors (one unmated) when female A approached them. Female B called whenever her prospective mate sang or was near her. After remaining 3–8 m from female B for about 3 min, female A began to follow her, sometimes approaching to within less than 1 m. Both females called Chek, apparently in response to the male's song and not at each other. Female B foraged rapidly, female A close behind. The only sign of agonistic motivation was a slight tensing by female B whenever female A alighted near her. After about 10 min I saw no further interactions. The two females began nest building on 12 May and 16 May and remained till the end of the season.

To summarize, females were capable of most or all visible aggressive displays of males and performed them almost exclusively, but very rarely, intrasexually. Their general tolerance, which doubtless contributes to the Prairie Warbler's polygyny, implies an absence of strong competition for resources or male attention.

Spacing of nests by mates of polygynists.—The mean distance between 36 simultaneously active nests of females with the same mate was about 125 m, the minimum 50 m (p. 135). As suggested (p. 135), females probably knew the

general if not the exact location of nests of their male's other females and may have avoided building near those nests. If so, Prairie Warblers achieved without fighting the effect female Redwings attain by establishing inner territories (Orians 1961: 294). Possible advantages of spacing are discussed on pages 340 and 493.

DISCUSSION OF PRAIRIE WARBLER'S POLYGYNY

Instability of sexual bonds, in this Prairie Warbler population associated with and possibly in part caused by heavy nest losses, is a feature not previously discussed in connection with polygyny in passerines. The effect of the instability was probably to increase the frequency of polygyny by producing a supply of females seeking mates at times when many males had no young and minimal associations with their first females. Further, a consideration of great importance was introduced into many of the situations in which females chose mates. That consideration is the amount of time remaining in the breeding season. Most polygynous bonds were formed in midseason, when few unmated males were available. A key assumption in accounting for polygyny is that females discriminate among males and that "[i]n order for discrimination to be selected for, it is necessary that the failure to accept one mate will be followed by an opportunity to mate with other individuals with such a high probability that the loss in reproductive output resulting from the rejection of a potential mate is, on the average, less than the average gains that can be realized by obtaining a mate of superior fitness . . ." (Orians 1969: 591). To the sexually competent female Prairie Warbler, unmated in midseason with time running out and the pool of potential mates dwindling, rejection of a courting male solely because he was mated might assure reproductive failure for the year. That fact, plus the low probability that any mated male she chose would have simultaneous and in-phase broods to care for, would reduce pressure to seek a highly superior male or territory. Under these circumstances the margin of personal or territorial superiority usually thought to be necessary for a male to become a polygynist might in theory dwindle to zero; yet selection for polygyny could still exist.

That females did in fact seek superior males or territories in the population studied is indicated by the larger territories and shorter pre-pair-formation periods of polygynists. It also appears significant that females choosing mated males to pair with did not suffer lowered reproductive success as a result, as far as can be judged. And it is possible, of course, that their male progeny inherited superior reproductive potential from polygynist fathers.

CHAPTER 32

THE BROWN-HEADED COWBIRD AND THE PRAIRIE WARBLER

COWBIRD BEHAVIOR ASSOCIATED WITH LAYING

Preliminary examination of host nest.—I twice saw female cowbirds inspect Prairie Warbler nests, apparently as a preliminary to parasitizing them. (1) At 1017 on day 2 of the incubation period a male and female cowbird landed 4–5 m from a nest. The male flew on, and the female hopped aimlessly, probably not seeing the nest; when 1.3 m from it, she looked down and seemed to see it, gave several calls, and flew away. Next morning the nest contained a cowbird egg. (2) At 1235 on the last day of active building of a nest, a female cowbird flew to it, inserted her head for a few seconds, and flew away calling. The nest was too high to inspect and failed before hatching.

Hour of laying; behavior.—I saw 4 cowbirds go to Prairie Warbler nests to lay; 3 laid, but 1 saw me and left. Times of arrival of these birds were 0508, 0520, 0523, and 0523 (mean 0519); respective intervals between civil twilight and arrival were 14, 17, 13, and 11 (mean 14 min). In addition, 4 times at dawn I went to Prairie Warbler nests to watch warblers lay and found that cowbirds had already laid that morning; I arrived at 0502, 0505, 0510, 0535; these times were 9, 3, 23, 37 min, respectively, after civil twilight.

Female cowbirds that laid as I watched stayed on the host nest 22, 30, and 40 sec (compare Hann 1941; Mayfield 1960: 164–171). Three of the four flew directly and silently to the nest and departed in the same way; behavior of the other was as follows: A loud cowbird whistle preceded her arrival; about 30 sec later she went to within 10 m of the nest, after 10 sec flew to the nest tree and landed 1 m below the nest. The female warbler was present, having spent the night there; she had risen and hopped to the rim as the cowbird landed. When the parasite hopped up to nest level, the warbler flew away silently (compare Hann 1937: 202). The cowbird perched on the rim, spied me, watched me for 10 sec, hopped 0.5 m from the nest, quickly returned to the rim, and after alternately looking at me and the nest for 25 sec flew away. The warbler returned 13 min later, laid, and incubated.

Once a female cowbird removed a warbler egg immediately before a cowbird laid an egg. At 0521 the cowbird flew to the nest, then perched beside it for 10 sec looking in. She jumped to the rim, took an egg in her bill, and flew away with it after a total of 25 sec on the rim. About 30 sec later a female cowbird came and laid; her route to the nest was the exact reverse of the route by which the egg-removing bird had left. Because apparently two different females (see p. 374) parasitized this nest, it is uncertain whether one individual removed and then laid; but the timing and other circumstances suggest that the same female was involved.

Date of laying.—Table 120 shows the distribution, according to 5-day intervals, of the laying of 135 cowbird eggs in Prairie Warbler nests (1952–1969). Extreme

TABLE 120
DATE OF LAYING OF 135 COWBIRD EGGS IN PRAIRIE WARBLER NESTS

Date of laying	Cases	
	N	%, cumulative
May 1-5	4	3
6-10	13	13
11-15	22	29
16-20	26	48
21-25	19	62
26-31	19	76
June 1-5	9	83
6-10	7	88
11-15	7	94
16-20	3	93
21-25	4	99
26-30	0	99
July 1-5	2	100

dates were 4 May and 6 July; 103 eggs were laid in May, 30 in June, and 2 in July. The median cowbird laying date was 21 May, the mean 24 May (SD 13 days), and the modal 5-day interval (19% of eggs) 16-20 May.

The earliest date of a cowbird's parasitizing any host on the study area was 23 April; eggs were laid in April (usually in nests of the Rufous-sided Towhee) in about half the years. (The earliest date on which a Prairie Warbler laid was 2 May; see p. 184.) The latest cowbird laying was about 19 July, a few days earlier than the latest Prairie Warbler laying (25 July); but whereas cowbirds seldom laid in July, Prairie Warblers did so rather often (Chapters 20 and 34).

TABLE 121
TIMING OF LAYING OF 109 COWBIRD EGGS IN RELATION TO TIMING
OF LAYING OF EGG 1 BY PRAIRIE WARBLER HOSTS

	Cases
Laid before egg 1	
Warbler deserted, no egg 1	8
5 days	1
4 days	2
3 days	6
2 days	6
1 day	6
Total	29
Laid same day as egg 1	
Total	9
Laid after egg 1	
1 day	29
2 days	20
3 days	7
4 days	4
5-12 days	11
Total	71
Grand Total	109

TABLE 122
STAGE OF REPRODUCTION AT HOST NESTS WHEN COWBIRD LAID

Stage	Cases	
	N	% ²
Active building ¹	4	3
Inactive building ¹	26	21
Laying interval		
Day 1	11	9
Day 2	27	22
Day 3 ²	20	17
Final day ³	7	6
Day not certain	11	9
Incubation period		
Day 2 ²	5	4
Day 3	1	1
Day 4	4	3
Day 7	3	2
Day 9	2	2
Total	121	100

¹ These terms are defined on page 149.

² Percents as rounded do not total 100.

³ See page 199 for treatment of 3- and 5-egg clutches. The day after that on which the final warbler egg was laid is day 2 of incubation.

About 76% of cowbird eggs in Prairie Warbler nests were deposited in May and 94% before 16 June (Table 120). Proportions of warbler eggs laid by these same dates were considerably smaller (e.g. see the distribution in Table 135, p. 398). Thus, intensity of parasitism waned in June and July, and later warbler nests suffered little cowbird interference (compare Hofslund 1957).

Timing of laying by individual cowbirds relative to laying by host warblers.—

In 109 cases I knew the day on which a cowbird laid in a warbler nest and the day on which the host female laid egg 1. All nests were under observation before any eggs were deposited, but a possible source of error is that most cowbirds removed warbler eggs from their victims' nests (see p. 375). If egg 1 had been removed before my inspection on the day it was laid, I might have thought laying began the following day.

Of 109 cowbird eggs, 38 (35%) were laid before warbler egg 1; of these, 29 were laid before the day on which the host laid egg 1 and 9 on the same day as egg 1 (Table 121). I have assumed that when a cowbird and a warbler laid on the same day the cowbird laid earlier (see hours of laying, pp. 189–193, 371).

The remaining 71 cowbird eggs (65%) were laid after the warblers had begun to lay and in some cases after their clutches were complete (see below). In 4 of these cases the warbler nest had failed before the cowbird laid; 2 of the 4 were empty and 2 held abandoned warbler eggs.

The 11 eggs laid long after incubation began (5–12 days; see Table 121) include 3 laid 5 days after warbler egg 1, 3 laid 6 days after that egg, 1 laid 8 days after, 2 laid 9 days after, 1 laid 11 days after, and 1 laid 12 days after.

Stage of host's reproduction when cowbird laid.—This analysis (Table 122) is necessary because the stage of the warbler's reproduction at the time her nest was parasitized cannot always be inferred from the data in the preceding sub-

TABLE 123
NUMBER OF PRAIRIE WARBLER EGGS¹ REMOVED PER PARASITIZING COWBIRD

Eggs removed per female cowbird ²	Cases	
	N	%
0	19	20
1	64 ¹	67
2	10	10
3	1	1
4	2	2
Total	96	100

¹ Included is a cowbird egg; it disappeared from a nest apparently parasitized by 2 female cowbirds (see footnote 2).

² If 2 warbler eggs disappeared from nests apparently parasitized by more than 1 cowbird (see text, this page), each cowbird is assumed to have taken 1 egg.

section. For example, a cowbird egg deposited 3 days after warbler egg 1 would be laid probably 10–30 min before the final warbler egg of a 4-egg clutch but on the second day of incubation of a 3-egg clutch.

The sample (121) includes cowbird eggs whose dates of laying were not known to the day but were known to be within the host's inactive building phase (see p. 149) or laying interval. Seventy-six (63%) cowbird eggs were laid during the warbler's laying interval; 26 (22%) others were deposited during the inactive building phase; 4 (3%) were laid during active building and 15 (12%) after incubation had begun (including after failure of nests). Counting only eggs laid during active building and after incubation began, about 16% of all cowbird eggs were laid at inappropriate stages in the host's cycle; they died (compare Mayfield 1960: 156–159; see p. 396). Even this figure may underestimate the inefficiency of the mechanism that synchronizes cowbird laying with the host's reproductive cycle: many warbler nests suffered predation during laying or early in incubation (Chapter 33), which would reduce the cowbird's opportunities to make mistakes, i.e. to lay in the incubation period.

Laying by two cowbirds in one day.—Three times nests received 2 cowbird eggs on 1 day (compare Mayfield 1960: 160), twice on the day the host laid egg 3, once on the day of egg 2. These cases can safely be assumed to have involved different female cowbirds. When a nest was parasitized more than once but on different days I refer to parasitism by “apparently the same” female or “apparently different” females, basing this judgment on similarity or dissimilarity of egg markings, color, and size.

COWBIRD REMOVAL OF WARBLER EGGS

Frequency, number taken.—Data are taken only from parasitized nests, ignoring occasional nests from which a marked warbler egg disappeared or in which an expected warbler egg was not found (see p. 189), but no cowbird egg ever laid. Also excluded, because the female cowbird did not have the normal opportunity to remove a host egg, are cases in which presence of the cowbird egg evidently caused the warbler to abandon before laying, a cowbird egg was laid after a predator had emptied the nest, or a predator removed all host eggs within a few hours after the cowbird's laying.

TABLE 124
TIMING OF REMOVAL OF HOST EGG RELATIVE TO STAGE OF CYCLE
AT HOST NEST

Host stage at removal	Cases	
	N	%
Laying		
Day 1	4	5
Day 1 or 2	12	15
Day 2	24	31
Day 2 or 3	10	13
Day 3	11	14
Day 3 or 4 ¹	3	4
Incubation		
Day 1 ¹	5	6
Day 2	1	1
Day 2 or 3	1	1
Day 3 or 4	1	1
Day 4	3	4
Day 6 or 7	1	1
Day 7 or 8	1	1
Day 9	1	1
Totals	78	100²

¹ See pages 375-376 for methods.

² Percents as rounded do not total 100.

Whenever parasitism was followed within 1 day by the disappearance of host eggs, however many, and the cowbird egg remained, I assume a cowbird was responsible. When apparently different cowbirds laid in a nest and two or more eggs disappeared, I assume each cowbird took at least one host egg; this assumption is based on the evidence (below) that from nests parasitized once most cowbirds did take a host egg.

A source of possible error is that if warbler egg 1 disappeared before I found it, I might mistakenly conclude that no egg had been deposited that day and underestimate the frequency of removal.

Of 96 parasitizing female cowbirds that had opportunity to take eggs, 19 (20%) took none and 77 (80%) took 1 or more (Table 123). Within the latter group, 64 (83%) took 1 egg, 10 (13%) took 2, and 3 (4%) took 3 or 4. The 96 females removed 94 warbler eggs and 1 cowbird egg (see below) and laid 97 eggs (0.98 eggs lost for every parasite egg laid); compare Hann 1937: 204, Hofslund 1957, and Mayfield 1960: 160-164, 181.

Hour of removal.—The only instance in which I saw a removal, at 0522, is described above (p. 371). In another case removal was between 1415 and 1900. Mayfield (1960: 160) states that the act usually occurs before 0900 but not at the time of laying; thus both times reported by me were atypical (see also Hann 1941).

Stage of host's nesting effort.—The timing of removal relative to stage of the host's reproduction is known to the day in some cases, to within 2 days in others. As a typical example of the latter kind of data, egg 2 sometimes disappeared between midday inspections on the second and third days of laying. Table 124 subdivides the data according to their two degrees of precision but does not

distinguish between nests that lost one egg and nests that lost more than one; in the few instances (below) in which removals occurred on more than 1 day, the word "or" must be read "and."

The day on which the warbler laid her final egg was also day 1 of the incubation period. The situation at the nest that day was more like that on other days of incubation than other days of laying (e.g. with respect to the probability of the female's being present if a cowbird came to remove an egg); therefore an egg removed on that day is counted as taken on day 1 of incubation. If removal could have been on either the day of laying the next-to-last or the last egg, it is arbitrarily assigned to the laying interval.

Most removals, including 22 of the 28 cases in which disappearance could be fixed only within 2 days, were during the laying interval; at least 62% of all laying-interval removals were on day 1 or 2. Fourteen (18%) nests lost eggs after incubation had begun.

In 13 instances a cowbird took 2 or more eggs (Table 123), 7 of these 13 on or after day 2 of the incubation period. Only 9 nests among the 78 (Table 124) were parasitized during incubation; thus cowbirds appeared to take more host eggs when they parasitized at that stage. Removal behavior may involve evaluation of the results of removal; the cowbird may reduce the number of eggs to an incomplete clutch, such as would be present midway in the laying interval (compare Mayfield 1960: 161-162).

Interval between multiple removals.—At 7 nests 2 eggs were taken on the same day; at 6 nests multiple removals were spread over 2 days; at 2 nests the timing was not clear. The foregoing numbers total 15, although only 13 nests lost 2 or more eggs, because 2 nests fall into more than one of the categories.

Timing of removal relative to cowbird's laying.—Treating each taking as a separate case, I know to within either 1 or 2 days the interval between a cowbird's laying and removal. Most instances in which apparently different females took an egg could not be used because a particular removal could not be associated with a particular laying. I have included multiple-taking cases only when two females laid or removed on the same day (see the assumption, p. 375).

Between 28% and 57% of 72 removals were on the day the parasite laid (Table 125); in evaluating this figure, note that 29 cases of cowbird laying (27%) among the 109 layings analyzed (Table 121) occurred on a day before the host began to lay, i.e. when it was impossible for the parasite to remove a host egg on the same day. At least 19% of the host eggs were taken 1 or more days after the cowbird laid; in the extreme case, a parasite laid as a nest was completed, and a host egg disappeared 1 week later. Finally, at least 24% of the warbler eggs were taken on a day before the cowbird laid (compare Hann 1937: 202-204, 1941; Mayfield 1960: 160-164).

Cowbird discrimination among own and host eggs.—The 78 cases (Table 124) are distributed among 3 classes: Some nests contained only Prairie Warbler eggs at the time of removal, some both warbler egg(s) and cowbird egg(s), some certainly warbler egg(s) and possibly cowbird egg(s). Considering the early hour at which cowbirds laid (p. 371), they must rarely have removed an egg in the brief daylight interval before laying (Mayfield 1960: 160), even though I saw this once. For that reason when a cowbird laid and removed on the same day,

TABLE 125
TIMING OF REMOVAL OF PRAIRIE WARBLER EGG BY COWBIRD, RELATIVE
TO LAYING OF COWBIRD EGG

Removal	Cases	
	N	% ¹
Before laying		
2 days	3	4
1 or 2 days	6	8
1 day	8	11
1 day before or day of laying	16	22
Day of laying	20	28
Day of laying or 1 day after	5	7
After laying		
1 day	3	4
1 or 2 days	2	3
3 days	2	3
3 or 4 days	2	3
4 days	1	1
4 or 5 days	2	3
5 or 6 days	1	1
6 or 7 days	1	1
Totals	72	100

¹ Percents as rounded do not total 100.

I assume laying preceded removal except in the one observed case. This assumption increases, of course, the number of cases in which I believe cowbirds had to choose whether to remove a cowbird or a host egg.

In at least 21 (27%) of 78 nests, only Prairie Warbler egg(s) were present at the time of removal. In at least 46 nests (59%), eggs of both species were present; only warbler eggs were removed (compare Hann 1957: 204 with Mayfield 1960: 164). In one case (1%) to be described below, a cowbird evidently took a cowbird egg, possibly the only egg present. Finally, in 10 cases (13%) Prairie Warbler eggs were taken, but it is not clear whether a choice had to be made.

Three removals were on the day the host laid egg 1 and before the cowbird had laid. Thus the nest was left empty until next morning (compare my experimental removals, p. 175), a situation which Mayfield (1960: 161) and Hann (1941) did not observe in their studies.

That a cowbird would occasionally take an egg of its own species, possibly when there was no alternative, is suggested by the following: On 7 June a cowbird laid in a newly completed nest. Warbler egg 1 was laid on 10 June. Between 0900 on 10 June and 0900 on 11 June, both these eggs disappeared; a second cowbird egg (apparently laid by a different female) and warbler egg 2 were laid in this same interval, presumably early on 11 June. Either a cowbird took a cowbird egg, possibly its own, when it had the option to take a warbler egg, or cowbird(s) removed two eggs on 10 June, one of them a cowbird egg.

Breakage and ejection of eggs.—At 83 warbler nests that held eggs when cowbirds laid and/or removed, I examined remaining eggs for damage. In 12 (14%) nests, eggs had been fatally punctured, cracked, or dented. In 2 of

TABLE 126
FREQUENCY OF COWBIRD PARASITISM OF NESTS,¹ ACCORDING TO DATE
OF PRAIRIE WARBLER EGG 1

Date	All nests	Parasitized nests	
		N	%
May 1-5	4	2	50
6-10	43	15	35
11-15	49	18	37
16-20	48	14	29
21-25	38	15	39
26-31	30	10	33
June 1-5	20	5	25
6-10	16	4	25
11-15	26	5	19
16-20	14	3	21
21-25	17	1	6
26-30	9	0	0
July 1-5	12	0	0
6-10	5	0	0
11-	5	0	0
Totals	336	92	

¹ The sample and methods are described on pages 378-379.

these, 2 eggs had been broken and in 10, one. Two of the 14 broken eggs were cowbirds'. Observed punctures were very tiny, and others may have been present and overlooked because they did not cause albumen to leak.

To compare breakage caused by laying with that caused by removal, I examined cases of breakage in which laying and removal were on different days. In 5, breaks apparently resulted from laying (6% of 79 layings), in 5 others from removal (6% of 82 removals). No type of damage was specific to laying or removal.

Once a warbler egg lay beneath a nest that held two newly laid cowbird eggs and a punctured host egg (compare Laskey 1950).

FREQUENCY OF PARASITIZATION OF PRAIRIE WARBLER NESTS

Percentage parasitized.—Mayfield (1960: Chapter 15, 1961) pointed out that a population's reproductive success cannot be estimated accurately from study of nests discovered after eggs have been laid. For the same reason the incidence of cowbird parasitism cannot be based on the number of cowbird eggs or young in nests found after the host has laid, although this mistake is not uncommonly made. I selected my sample as follows:

1. Nests containing a warbler egg when found were excluded.
2. Nests that failed to predators before the host clutch was completed were included, although such early predation may have forestalled parasitism that would otherwise have occurred. These inclusions probably bias the result; but the bias would be even greater if only nests with full host clutches were considered, because cowbird interference often caused Prairie Warblers to abandon without completing the clutch (see below). It is important that these latter cases not be ignored in selecting the sample. As an estimate (derived from Chapter

TABLE 127
OBSERVED AND EXPECTED¹ NUMBERS OF COWBIRD EGGS PER NEST
IN 336 PRAIRIE WARBLER NESTS²

Cowbird eggs per nest	Observed	Expected ^{1, 3}
0	244	247
1	80	76
2	12	12
More than 2	0	1

¹ Expected numbers were calculated from the Poisson distribution.

² The sample is described on pages 378–379.

³ Chi-square = 0.3; df = 2; $P \cong 0.90$. Values for 2 or more eggs were pooled for this test.

33) of the level of potential bias introduced by including nests preyed upon while clutches were incomplete, some 60–80 days of exposure to cowbirds, at about 40 nests were eliminated. Had all nests survived until all host eggs were laid, opportunities for cowbirds to parasitize the sample would have been greater by 5–6%.

3. Completed nests found during construction are included even if warbler eggs (and cowbird eggs) were never deposited, provided the apparent reason for the host's failure to lay was not damage to the nest. Parasitism itself caused several warblers to abandon without laying; in order to count these cases, all intact nests without eggs must be included.

4. Nests that cowbirds laid in after failure are excluded because I do not know how many others that failed did not receive cowbird eggs (i.e. I usually quit inspecting nests after their failure).

5. The sample is restricted to nests no higher than 3 m; daily inspection of higher nests was not possible.

The calendar distribution of the nests to be analyzed is representative of the distribution of all Prairie Warbler nests built during the study (compare dates of 608 nests in Table 46 and data in Table 126), a point of importance because parasitism varied according to date.

Ninety-two of the sample of 336 nests (27.4%) were parasitized while still in use.

Numbers of cowbird eggs per nest.—Nests in which 1 cowbird egg was laid numbered 80 and in which 2 were laid, 12, a total of 104 parasite eggs.

The question whether cowbirds single out some nests and avoid others has been considered by Preston (1948) and Mayfield (1960: 153–155, 1965a), who compared observed frequencies of parasitization with expected frequencies calculated from a Poisson distribution. Mayfield (1965a) noted that nests containing one cowbird egg, as reported by various investigators, were fewer than expected and attributed this to the usual biased method of determining rates of molestation (from nests found at all stages of the nesting cycle; see p. 378). He concluded that many nests parasitized only once are overlooked because they fail too quickly. Data on cowbird eggs per Prairie Warbler nest conform closely to expectations under the Poisson distribution (Table 127); my sample eliminates the bias referred to, and the good fit tends to support Mayfield's view.

Variation according to date.—Table 126 distributes the 336 nests (above) according to the 5-day calendar interval within which warbler egg 1 was laid in

TABLE 128
COWBIRD PARASITISM OF MAY¹ NESTS OF PRAIRIE WARBLER, ACCORDING
TO NEST HEIGHT

Height	Total nests	Nests parasitized	
		N	%
0-1 m	75	19	25
1-2 m	100	41	41
2-3 m	37	15	41

¹ Nests received egg 1 in May.

each. For the 18 nests in which no warbler egg was laid, a hypothetical egg 1 date was obtained by adding mean length of inactive building phase for the date (Table 49) to the date on which active building concluded.

In May the percentage of nests receiving cowbird eggs fluctuated (29%–40%) apparently without any pattern, omitting the inadequate subsample for 1–5 May, and I have therefore pooled data for that month; cowbirds laid in 74 of 212 nests (35%). The figure declined to 25% for 1–10 June and 20% for 11–20 June; thereafter it fell rapidly to 0. As stated, few nests were parasitized in late June and early July (p. 372); the absence of any July cases in Table 126 is the result of sampling error.

In a test of independence of parasitism and date, based on the 5 half-months between 1 May and mid-July, Chi-square = 21.4; df = 4; $P < 0.001$. This seasonal decline of parasitism appears to have been primarily the result of the cowbird's laying season, i.e. its concentration of egg-laying into May and early June. It cannot be accounted for by my sampling methods, and investigations of all breeding species on the study area indicate no switch from Prairie Warblers to other hosts in late June and July.

Eleven nests that were parasitized twice received warbler egg 1 no later than 21 May, the last on 29 May; dates of 1-egg parasitization and 2-egg parasitization did not differ significantly. Laskey (1950) suggested that in Tennessee multiple parasitization tended to be early because potential host nests were scarce at that time, but this explanation appears inapplicable to my data. Among the principal cowbird hosts on the area only the Indigo Bunting sometimes postponed nesting until as late as about 1 June; total nests of all host species probably did not increase much during the Prairie Warbler's breeding season, although changes in placement may have affected the cowbird's ability to find them.

Variation according to height.—Because both nest height (Table 42) and rate of parasitism changed with date, analysis is confined to May, when variation probably was absent. I have distributed the 212 May nests according to 50-cm intervals of height above ground.

Rates of parasitism, proceeding consecutively from nests at 0–50 cm to nests at 251–300 cm, follow: 22%, 26%, 39%, 44%, 33%, and 54%. Absolute numbers for extreme height intervals were 2 nests parasitized among 9 built at 0–50 cm and 7 parasitized among 13 built at 251–300 cm. To obtain subsamples large enough for a Chi-square test, height intervals were reduced to three, each of 100 cm (Table 128). The result is nonsignificant ($0.10 > P > 0.05$), but

the steady increase in rate with ascending height suggests that larger samples would show a difference. (Not included in the analysis are 12 nests higher than 3 m; 5 held cowbird eggs. See also evidence of reduced parasitism of ground nests of fringillids in May, Nolan 1963).

Variation according to stage of breeding cycle of host.—Methods: For presentation of daily rates, samples were selected differently for different stages of reproduction. At every stage the fact that a nest already held a cowbird egg was ignored, because parasitized nests were vulnerable to further parasitism. Nests higher than 3 m and those parasitized after failure were excluded. In determining the rate for any particular day, e.g. day 2 of the laying interval, nests that failed before that day were, of course, ignored.

For the active-building stage I estimated the number of days on which I examined incomplete structures that had progressed to the point of being fully shaped outer shells, i.e. structures that superficially looked ready for eggs; I then counted cases of laying in these. For the inactive phase, I tabulated inspections on which I found and inspections on which I did not find cowbird eggs present, treating nests that never received a warbler egg as having inactive phases of 5 days. No difference was evident in rate per day of inactive phase, and data from all such days were pooled.

Days of the laying interval were treated separately because parasitism varied according to day. The final day of laying was assigned to the laying interval rather than the incubation period because a cowbird visiting the nest very early on that or the preceding day would find the clutch incomplete; further, from the point of view of its survival, a parasite egg laid on that day would be incubated for almost the full period of the warbler. Because 4 was the modal clutch size I divided the laying interval into days 1, 2, 3, and final. For clutches of 3 eggs, the day egg 3 was laid was tabulated as the final day and no entry was made for day 3. For clutches of 5 eggs, days of laying both eggs 3 and 4 were tabulated under day 3 (compare p. 199).

I divided the incubation period subsequent to day 1 into 2 unequal parts, viz. day 2 alone and all later days pooled, because the data indicate that the rate on day 2 was higher than on subsequent days, which did not differ among themselves. This is not unexpected; if the optimal and modal time to parasitize is during the warbler's laying interval (see Tables 122 and 130), small deviations would be more likely than large ones. Subsamples for the incubation period were not restricted to nests discovered before laying; those found before or during incubation and observed before hatching for any multiple of 24 hours contributed a corresponding number of data on the daily rate. No cowbird egg was laid in a nest containing young; I estimated the number of days on which I inspected such nests.

Results: Rates were lowest during those stages of host reproduction in which the cowbird egg had little or no chance of survival (Table 129). From 0.008 eggs per day during active building the rate increased to 0.046 during inactive building. A decline on the day of laying egg 1 seems likely to be attributable to sampling error; the maximum rates (0.087 eggs and 0.074 eggs, respectively) on the days when host eggs 2 and 3 were laid probably reflect a genuine peak (see pp. 383–384, dealing with rates of host desertion). On the final day of laying

TABLE 129
DAILY RATE OF PARASITISM OF PRAIRIE WARBLER NESTS,¹ ACCORDING
TO STAGE OF REPRODUCTION

Stage	Days of exposure to cowbird ¹	Cowbird eggs received	
		N	Rate/day
Active building ²	520	4	0.008
Inactive building ²	561	26	0.046
Laying interval			
Day 1	337	11	0.033
Day 2	310	27	0.087
Day 3 ³	272	20	0.074
Final day ³	226	7	0.031
Incubation period			
Day 2	216	3	0.014
Day 3—hatching	1709	8	0.005
Nestling interval	about 1000	0	0.000

¹ Methods are described on page 381.

² Terms are defined on page 149.

³ See page 381 for treatment of 3- and 5-egg clutches. The day after that on which the final warbler egg was laid is day 2 of incubation.

the rate fell to 0.031, then to 0.014 on day 2 of incubation; the mean daily rate for the rest of the period was 0.005.

The behavior of the building female warbler and her prolonged presence at the nest during incubation could provide the necessary information to prevent most cowbirds from laying at those stages, as could the presence of young during the nestling interval. The sharp increase of parasitism on the morning the warbler was scheduled to lay eggs 2 and 3 may suggest that rapid development of the cowbird's ovum had been stimulated several days earlier by observation of nest building and/or that on the preceding day the presence of a host egg or eggs had made the cowbird aware that the host's laying had begun (see Hann 1941, Mayfield 1960: 164–171).

Annual differences.—The following fractions show numbers of parasitized nests among all warbler nests that received egg 1 in May in years in which I found at least 8 May nests; cases are taken from the 336 nests described on pages 378–379. In parentheses are numbers of nests that received two cowbird eggs: 1952—6 parasitized nests of a total of 9 (1); 1953—4 of 9 (1); 1954—2 of 10 (0); 1958—7 of 26 (0); 1959—9 of 25 (1); 1960—7 of 31 (1); 1961—11 of 23 (4); 1962—1 of 12 (0); 1963—5 of 10 (2); 1964—6 of 16 (0); 1965—5 of 8 (0); 1966—3 of 10 (0).

Multiple parasitization tends to be concentrated in years in which proportions of nests parasitized were largest. Because laying of a second cowbird egg appeared independent of the presence of a first (p. 379), the annual total of cowbird eggs can be divided by the number of May nests in that year to give an estimate of cowbird pressure. Percentages vary from 8% to 78%. The percentage (65%) calculated in this way for 1961 does not take account of the fact that at least 1 of the 12 nests listed as unparasitized in that year received a cowbird egg after it failed.

TABLE 130
FREQUENCY OF DESERTION OF NESTS BY PRAIRIE WARBLERS, ACCORDING
TO STAGE AT WHICH COWBIRD INTERFERED¹

Stage(s) ² at interference	Nests interfered with N	Nests deserted	
		N	%
Active building only; active building and laying interval	4	1	25
Inactive building only; inactive building and laying interval	18	10	56
Laying interval only	52	13	25
Inactive building and incubation period	1	1	100
Laying interval and incubation period	8	6	75
Incubation period only	10	7	70
Total	93	38	41

¹ Interference includes laying an egg with or without removal of warbler egg(s). Cases in which broken eggs were left in the nest are excluded.

² Interference consisting of 2 acts sometimes fell at different stages of the same nest; therefore some categories include more than 1 stage. Terms for phases of building are defined on page 149. The incubation period began the day the warbler laid her final egg.

Parasitism on sections of study area.—Nest height and probably nest success differed on the University Farm (studied 1952–1954) and the Griffey Tract (Chapters 15 and 33), but the annual data, above, do not suggest similar variation in parasitism. In a Chi-square test with annual totals of nests and of cowbird eggs for each tract pooled, the result is far short of significance.

PRAIRIE WARBLER REACTIONS TO COWBIRD INTERFERENCE

“Interference” includes laying unaccompanied by egg removal and also laying associated with removal; each case of either kind is counted as 1. Reactions of female warblers to interference were observed in 105 cases; another instance is excluded because a predator and a cowbird molested the nest nearly simultaneously.

Warblers deserted either immediately or before beginning to incubate after 48 (46%) interferences; details are given below. The other 57 parasitized nests (54%) continued in use, but 7 were emptied by predators before the host began to incubate. Because warblers sometimes delayed their reactions—they continued to lay but deserted without incubating—some or all of these seven nests might have been deserted had they escaped predation (see the following sections).

Desertion because of damage to remaining eggs.—The warbler always deserted if a broken egg leaked (10 nests) but not if contents of the eggs dried without leaking (2 nests).

Desertion and stage of nesting cycle at interference.—For numerical analysis I have eliminated nests in which eggs were broken, because that factor was overriding and usually caused desertion. When two or more cowbird acts (laying plus one or more removals) took place at different stages of the host's nesting cycle, that is shown in Table 130; sequence of these acts is ignored. The day on

which the warbler laid her final egg is treated as part of the incubation period (see p. 376).

Interference that began in or extended into the incubation period usually caused desertion (14 of 19 cases, or 74%; see bottom three rows of Table 130). The fact that often more host eggs were removed than (p. 376) may have contributed to this high rate; in 4 of the cases in which interference was tolerated there was no removal at all, but in the fifth a female continued to incubate despite removal of 2 of her eggs on day 7 of incubation.

Interference during inactive building (i.e. the cowbird laid in an empty nest) produced the second highest rate of desertion (56%): Six females deserted without laying; 2 laid egg 1, then deserted; 10 laid full clutches, 2 of these then deserting and the other 8 incubating.

Desertion was much less frequent (25%) when parasitism fell during the warbler's laying interval. When it occurred it was sometimes immediate, with no further laying by the host. Some hosts laid one more egg and deserted; two deserted after laying two or more eggs and bringing their clutches to full size.

Three of four females that were parasitized during active building went on building and used their nests. Two of the three eggs were embedded (see pp. 141–142). This unresponsiveness to foreign objects in nests under construction is consistent with experimental results described on pages 159–160.

Desertion related to removal of host egg or eggs.—Prairie Warblers appeared at least as intolerant of laying without removal as of laying accompanied by removal of one egg; removal of two eggs may have increased the desertion rate. To investigate whether desertion was affected by removal, I eliminated kinds of interference especially conducive to desertion (egg breaking and interference at stages other than the laying interval). There remain 14 instances in which 1 cowbird egg was laid with no removal, 34 in which 1 cowbird egg was laid for each warbler egg removed, and 4 in which 1 cowbird egg was laid and 2 warbler eggs removed.

Of the 14 nests not suffering removal, 3 (21%) were deserted. Of the 34 nests from which there was 1 removal per egg laid, 6 (18%) were deserted. Of the 4 nests with 2 removals and 1 egg laid, 3 (75%) were deserted. Removal of one warbler egg may have tended to reduce desertion, possibly by eliminating overcrowding. A parasitized five-egg warbler clutch, one egg of which was removed, was deserted; because of the cowbird egg's larger size and the number of warbler eggs laid (pp. 385–386), the nest was unusually crowded. Four nests were parasitized, then received full clutches, but subsequently were deserted. From 2 of these there was no removal; they held 4 warbler eggs and 1 cowbird egg and were thus abnormally crowded. I twice found newly abandoned nests with this same combination of eggs, fresh and evidently unincubated. But see the results of experimental introduction of eggs (p. 175).

In connection with the suggestion that double removals were especially likely to lead to desertion, see the reactions to my taking of parts of clutches (p. 175).

Rate of desertion according to date.—Some birds are reported more likely to desert early nests than late nests (Heinroth and Heinroth 1959: 39), but Prairie Warbler tolerance of cowbird interference appeared independent of date. Using all cases of interference during inactive building and/or laying, except those in which

eggs were broken or removals exceeded one warbler egg per cowbird egg laid, I compared rates of desertion in the four half-month intervals of May–June. Five of 21 nests (24%) parasitized in the first half of May were deserted, 11 of 32 (34%) in the second half of May, 3 of 9 (33%) in the first half of June, and 1 of 4 (25%) in the second half of June.

Age of female related to desertion.—Yearling females may desert more readily than older birds. Using the same sample as in the preceding paragraph and excluding nests of females of unknown age, of 19 yearlings 10 (53%) deserted, as against 6 of 26 (23%) old birds. In a test of independence Chi-square without adjustment = 4.2; $df = 1$; $P < 0.05$; adj. Chi-square = 3.0. Sokal and Rohlf (1969: 590) state that Yates' correction is unnecessarily conservative even when samples being tested are small.

EFFECTS OF PARASITISM ON PRODUCTION OF FLEDGLINGS

Percentage of success of parasitized nests.—Success of a nest is production of at least one fledgling warbler or cowbird; if no young left the nest it failed. Nests found before egg-laying began, inspected daily thereafter and parasitized before they failed, numbered 86. The fates of these were as follows: 44 (51%) were deserted after cowbird interference; 35 (41%) suffered predation; 1 (1%) failed either because of parasitism or predation; 6 (7%) produced fledglings (7 warblers and 5 cowbirds). The total of warblers produced by the successful nests would doubtless have been smaller had not a cowbird egg disappeared from one nest; the young warblers therefore had no cowbird nestmate to compete with (see below).

Hatching rate in parasitized nests.—In unparasitized nests, 95% of the eggs present at the end of incubation hatched (p. 407), in parasitized nests 92% (next paragraph); the difference is nonsignificant (compare Hofslund 1957, Mayfield 1960: 171–172). Both rates are based on eggs under observation throughout the hatching interval (defined on p. 239). Sometimes the total of eggs and/or young decreased during that interval. To illustrate, the contents of a nest when first inspected on hatching day were one warbler and one cowbird nestling and two warbler eggs; several hours later there were one cowbird and two warbler nestlings and no eggs. In such cases I have assumed that the missing animal disappeared after hatching, for these reasons: (1) So far as known, Prairie Warbler parents always removed dead nestlings, never dead eggs. (2) Predators that took only part of a nest's contents seemed to prefer nestlings to eggs (see below); even when predators had no preference, eggs would be likely to be covered by nestlings and therefore less noticeable to a predator.

Fourteen nests held 38 warbler eggs and 17 cowbird eggs when hatching began; 3 warbler eggs (8%) did not hatch. Four cowbird eggs (24%) also failed to hatch, but 3 had been laid midway in the incubation period and probably died because they were insufficiently incubated.

Hofslund (1957: 42–44) worked out volumes of Common Yellowthroat and cowbird eggs and various combinations of these and concluded that "1.3 times the normal clutch volume closely represents the limit of egg-volume that a Yellowthroat will normally hatch. . . ." I calculated the mean volume of 42 cowbird eggs (see formula, p. 177) and found it to be 3.012 ml (SD, 0.279 ml). Since the mean

volume of a Prairie Warbler egg was 1.211 ml (Table 59) and of a 4-egg clutch 4.822 ml, addition of a cowbird egg unaccompanied by removal would increase clutch volume 1.62 times, to 7.856 ml. Nevertheless, 11 eggs hatched in all observed nests (3) containing 1 parasite and 4 host eggs when hatching began. Even a clutch containing 1 cowbird egg and 3 warbler eggs has a mean volume (6.645 ml) 1.37 times that of a 4-egg unparasitized clutch. Thus the Prairie Warbler's "hatching potential" (see Friedmann 1963: 21–22) evidently exceeds the yellow-throat's.

Many observers have seen host eggs covered by half the shell of a cowbird egg and have discussed whether this partial encasing prevents hatching (see Hann 1937: 204, Hofslund 1957). In my only observed case the warbler egg hatched but probably not as soon as it otherwise would have. Egg 1, which usually hatches first (p. 238), was found trapped by a cowbird egg shell at 1345. By 0900 next day, warbler eggs 2 and 3 had hatched; egg 1 hatched that night, at least 30 hours after being trapped and 19 hours later than eggs 2 and 3. Delayed hatching probably almost always dooms a Prairie Warbler if it has a cowbird nestmate (see below).

Development of young cowbird.—Many harmful effects of the young cowbird on the Prairie Warbler are attributable to its earlier hatching, larger size, and rapid growth. Data on development of cowbirds fostered by Prairie Warblers will be presented as background to analysis of warbler survival. The data should be compared with those on warbler development (Chapters 23, 26, 27, and 28).

Incubation period: Few who write about the length of the cowbird's incubation period define its starting point; Mayfield (1960: 177–178) is an exception. Presumably most writers measure from laying of the final host egg, which will be accurate only if the cowbird egg and last host egg were laid on the same day or if the host did not incubate until laying her last egg. Since Prairie Warblers usually began to incubate on the evening before laying the final egg (Chapter 21), I measured the cowbird's incubation period from 1930 on that day. However, most female warblers also spent some time on the nest before beginning full-scale incubation (Chapter 21), and my measurements may underestimate the cowbird's incubation period slightly. Periods were rounded to the nearest 0.5 hour; margins of error in hours were calculated and are presented as described on page 235.

The following 9 periods are arranged with the shortest first, ignoring margin of error: 269.0 (m.e. 10 hours), 274.0 (m.e. 11), 277.5 (m.e. 0), 282.0 (m.e. 3), 283.0 (m.e. 0), 285.0 (m.e. 0), 292.0 (m.e. 11), 292.0 (m.e. 12), 302.5 (m.e. 0). The mean, ignoring margin of error, is about 284 hours or 11.8 days (compare Hann 1937: 204, Hofslund 1957, Mayfield 1960: 177–178). Once an apparently living cowbird egg was destroyed by a predator 306 hours after incubation began; hatching of the host eggs was also overdue (see p. 236 for the circumstances).

Cowbird eggs always hatched before warbler eggs unless laid after incubation had begun. Usually the cowbird hatched between my nest inspections about 24 hours apart, and the first warbler egg hatched during the next 24 hours; the young cowbird appeared to be about 1 day old when the warbler was a few hours old. The most precisely known intervals between hatching of the cowbird and the first

warbler were these (in hours, shortest first): 5 (m.e. 3), 13 (m.e. 8), 24 (m.e. 2), and 26 (m.e. 2). Hours between hatching of the cowbird and the last warbler to hatch in 5 cases were 46 (m.e. 12), 35 (m.e. 6), 27 (m.e. 3), 25 (m.e. 2.5), more than 30 (compare p. 239). Female warblers generally spent less time incubating after young hatched (see p. 254), and the cowbird's earlier hatching probably delayed hatching of the warblers (see Mayfield 1960: 171–172).

Nestling interval: Twice cowbirds left nests at least one day before nestmate warblers (one of which was then abandoned by the parents), and twice host and parasite young left on the same day. Two cowbird nestling intervals lasted about 241 and 215 hours; 2 others lasted 216 and 222 hours, both with 6-hour margins of error. I removed 2 cowbirds from 1 warbler nest when they were 215 hours old; circumstances (hour of day, weather) made it unlikely that they would have left it before age about 230 hours (compare Hofslund 1957, Mayfield 1960: 179).

Nestling weights: Charles F. Thompson, G. Bruce Williamson, and I weighed cowbirds on an analytical balance immediately after they hatched in an incubator. Of 5 weights, extremes were 2.52 g and 2.17 g and the mean was 2.33 g. The following are mean weights at approximate indicated ages of three cowbird nestlings in Prairie Warbler nests: 12 hours—3.0 g; 36 hours—5.0 g; 60 hours—8.4 g; 84 hours—12.5 g. One of these same birds at age 108 hours weighed 16.0 g; at 132 hours, 23.1 g; at 162 hours, 28.3 g (compare Mayfield 1960: 178).

Period of dependence: Three periods of dependence of cowbirds tended by Prairie Warblers lasted at least 23 days, 25 days, and 30 days (compare Hofslund 1957 and 1959: 169 with Mayfield 1960: 180).

Success of warbler nestmates of cowbirds.—Nest predation was so high (Chapter 33) that only eight observed parasitized nests survived from hatching until nest-leaving. In these 19 warblers and 9 cowbirds had hatched; 4 warblers (21%) and 7 cowbirds (78%) left the nests. After hatching, 2 (22%) of the 9 cowbirds were taken by predators (see below).

Information about how cowbirds caused warbler nestmates to die was obtained from parasitized nests found at any time prior to death of the warblers. Young warblers usually did not gain weight normally (see Chapter 26), and most deaths probably were caused by starvation; suffocation, crushing, insufficient contact with the female's body (i.e. cooling) may often have contributed. One cowbird left the nest at normal age, and its one surviving warbler nestmate, weak and underdeveloped, was abandoned and allowed to starve. Falling from the nest because it was overcrowded was observed once: Three warblers and 1 cowbird seemed in good condition, though very crowded, 5 days after the warblers hatched; next day the cowbird and 1 warbler were left, with 2 dead warblers under the nest.

Approximate ages at death (in days, counting hatching day) of the 15 warblers that died in the 8 nests observed throughout incubation are shown in Table 131, as is cumulative mortality with advance of the nestling interval. A bird is treated as having survived a full day if it was alive when I made my inspection that day. Death was rare on hatching day, and most frequent during days 2–6; but 2 of the deaths on day 6 were caused by the case of crowding, reported above, and that

TABLE 131
SURVIVAL OF NESTLING PRAIRIE WARBLERS WITH COWBIRD NESTMATES,
ACCORDING TO DAY OF NESTLING INTERVAL

Prairie Warbler eggs hatched	Daily ¹ and cumulative survival ² of nestlings																	
	Day 1		Day 2		Day 3		Day 4		Day 5		Day 6		Day 7		Day 8		Day 9	
	N ²	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
19	18	95	15	79	12	63	10	53	9	47	6	32	5	26	4	21	4	21

¹ Day 1 is the day the warbler hatched, determined independently for each member of 8 clutches.

² N is the number of the original 19 birds still alive on each day. See pages 387-388.

may have been unusual. One bird died as late as day 8. The nest in which a nestling was allowed to starve is not tabulated because I did not discover it prior to hatching.

The last nestling to hatch probably usually died first, particularly if it hatched as much as 1 day after its siblings. I observed this in a nest in which I marked nestlings as they hatched, and there was indirect evidence from other nests.

Factors tending to reduce harmful effect of cowbird.—Although early hatching and greater size gave cowbirds a net advantage over warblers, I observed associated disadvantages that I have not seen described elsewhere: Some predators that discovered nests during the hatching interval took only nestlings, leaving any unhatched eggs. Six times I found living eggs in warbler nests from which all hatched young (three were cowbirds) had been taken. Four of these nests, including the three that had held cowbirds, continued to be cared for by parents and produced fledglings. In two comparable cases, all warbler nestlings were taken and dead warbler eggs were left. This total of eight nests in which only nestlings were selected by predators indicates that the risk of hatching earlier than nestmates is not negligible. A predator that may have been involved is suggested by an experiment: I put a nest containing three eggs and one nestling Field Sparrow by an Eastern Chipmunk den. A chipmunk emerged and ate only the nestling (see p. 415).

A somewhat similar probable disadvantage to cowbird nestlings is their greater size. A predator finding a nest holding a cowbird and warblers probably would seize the most conspicuous and topmost bird first. If this occurred late in the nestling interval, some nestlings would have a chance to jump out and escape, which apparently happened once: On the evening before nest-leaving was expected, a nest was pulled from its site; the cowbird that had been in it was missing, and the one warbler from it was nearby unharmed.

Number of fledglings from parasitized nests.—Production from 9 successful (defined on p. 385) parasitized nests selected because they produced cowbirds was 7 warblers (0.78 per nest) and 10 cowbirds (1.11 per nest). Sometimes, as in the preceding paragraph, cowbirds that did not survive to leave the nest were responsible for deaths of host eggs and/or nestlings before dying themselves. Data that take this fact into account would appear to provide a better estimate of productivity (of both host and parasite) from parasitized nests than data derived only from nests that produced cowbirds. For this purpose I have pooled the nine nests that produced cowbirds and the two nests that succeeded after cowbirds in them died, although this pooling combines cases selected by considerably different

TABLE 132
NUMBER OF FLEDGLINGS FROM SUCCESSFUL NESTS IN WHICH NO COWBIRD
EGG WAS LAID, ACCORDING TO DATE OF EGG 1

	Date of egg 1					Totals (76 nests)
	1-15 May (17 nests)	16-31 May (12 nests)	1-15 June (14 nests)	16-30 June (15 nests)	July (18 nests)	
Fledglings per brood						
5	1	0	0	0	0	1
4	10	9	7	5	3	34
3	6	1	6	7	12	32
2	0	2	1	3	3	9
1	0	0	0	0	0	0
Brood size						
Median	3.8	3.8	3.5	3.1	3.0	3.41
Mean	3.7	3.6	3.4	3.1	3.0	3.36
SD	0.59	0.79	0.65	0.74	0.59	0.71

standards. The 11 nests produced 0.91 warblers and also 0.91 cowbirds per nest. Subsequent references to production will specify whether 0.78:1.11 or 0.91:0.91 is the ratio used.

Number of fledglings from unparasitized nests.—Because cowbirds sometimes disappeared from nests that succeeded, the sample is limited to 76 successful nests found before laying and known never to have been parasitized. Table 132 shows brood sizes from these (overall mean 3.36) according to the half-month within which egg 1 was laid. (See Table 142, p. 410, for brood sizes of all successful nests, unparasitized and parasitized.) When successful unparasitized and parasitized nests are compared, it is seen that production of 0.91 cowbirds was at the cost of 2.45 warblers, a 73% reduction from mean brood size in unparasitized nests. The reduction would be somewhat greater if mean brood sizes in May and early June were used in the comparison (because most parasitism occurred then).

It is interesting also to compare the 76 unparasitized nests with 12 successful nests found after hatching and containing only Prairie Warblers when found: Five of the latter produced 3 warblers each; 5, two warblers each; and 2, one warbler each (mean brood size 2.25). Some of these 12 nests, with their lower mean production, may have held cowbirds that had died before I found them. If the output of the 12 is added to that of the 76 unparasitized nests, mean brood size (3.21 warblers) from 88 nests that produced no cowbirds can be compared with mean brood size from nests that did produce cowbirds (0.78 warblers, 1.11 cowbirds). The difference, 2.43 warblers per nest, is a reduction of 76%.

Survival of warblers after nest-leaving.—Fledgling warblers whose parents tended cowbirds did not appear to suffer thereby. Because of broods' separation into family units (Chapter 28) and low production of warblers from parasitized nests, fledgling warblers and cowbirds rarely were dependent on the same adult.

Success rates of parasitized and unparasitized nests.—In addition to measuring percentages of nests and/or eggs that yielded warbler fledglings, I determined the active life in days of parasitized and unparasitized nests. Active life began the day warbler egg 1 was laid and ended with the day the nest ceased to be used. Most successful nests had active lives of 24–25 days. For nests that failed between

inspections on successive days I assumed that failure occurred on the day I learned of it. Lengths of active life were not normally distributed either for parasitized or unparasitized nests (see Chapter 33).

Two different samples were analyzed. They were alike in that all nests were found before laying began and were inspected daily; no nests from the abnormal year 1956 (see p. 1) are included. One sample consists of May nests that were the first of the year for the females that built them. The second consists of all nests that received or would have received egg 1 prior to 21 June. Parasitism after 21 June was light, while at the same time reproductive success began an increase in part unrelated to reduced cowbird interference (see Chapter 33); inclusion of post-21 June nests would bias the estimate of the impact of parasitism.

Among May nests, 105 were unparasitized and 61 parasitized. Twenty (19%) unparasitized nests succeeded compared to 4 (7%) parasitized nests. Adj. Chi-square = 3.9; $df = 1$; $P \approx 0.05$. The median active life of unparasitized nests was 9.8 days (mean 10.5 days) and of parasitized nests 4.2 days (mean 7.1 days). The combined median was 6.3 days; in a median test, adj. Chi-square = 7.7; $df = 1$; $P \approx 0.005$.

Of nests receiving eggs prior to 21 June, 200 were unparasitized and 86 parasitized. Thirty-seven (19%) unparasitized nests succeeded compared to 6 (7%) parasitized nests. Adj. Chi-square = 5.4; $df = 1$; $P = < 0.025$. The median active life of the unparasitized nests was 9.7 days (mean 10.9 days), of the parasitized nests 4.1 days (mean 7.0 days; see p. 411). The combined median was 7.1 days; in a median test, adj. Chi-square = 19.2; $df = 1$; $P < 0.001$.

Calculations on page 411 indicate that the reduced success of parasitized nests was directly attributable to desertion by hosts; the presence of cowbird eggs and nestlings did not increase the predation rate.

Effect of cowbird on Prairie Warbler's production.—The simple and direct way to investigate the impact of the cowbird would be to compare production of female Prairie Warblers that escaped parasitism for a full season with that of the female population as a whole. This method cannot be used because information is incomplete for the many females that built one or more nests too high to inspect or spent only part of the season on the study area (Chapters 30 and 31). Unparasitized females whose full seasonal histories I know do not form a representative sample (see Chapter 33). Therefore investigation of the cowbird's effect requires more complex methods.

Calculated production—methods: I have calculated production of hypothetical populations using simulation and applying observed central tendencies and percentages. One hypothetical population is 100 females living under the conditions of my study area, except that cowbirds are absent; the other, to serve as a control, is 100 females living under all conditions of my study area. Calculated production of this latter group can be compared with observed production on the study area as some check on the reliability of the simulation. For simplicity, the method will first be described for the unparasitized population. For directness, the description will be written as though reporting actual observations:

1. Laying started on 14 May, the mean of 14 annual mean dates (Table 63).

2. Percentage of nest success was determined from rates for 200 unparasitized

nests in the sample described on pages 378–379. Because rate varied with date, I selected 10 dates at approximately equal intervals over the full season, tabulated all nests that received egg 1 within a 15-day period of which each selected date was the middle day, and obtained the success rate for each period. The 15-day periods overlapped. Sample size per period was 30 or more in May and June, 20 or more between 1 July and 10 July, 10 or more between 11 July and 15 July, and 3 after 15 July. When the curve of success rates for the 10 periods was smoothed, resulting percentages used in the simulation were these: 14 May–10 June, 18%; 11 June–20 June, 22%; 21 June–5 July, 24%; 6 July–10 July, 27%; 11 July–15 July, 36%; 16 July–end, 67%.

3. Median active life of unsuccessful nests was obtained from the same 15-day-period samples. The median for May nests was 7 days, for nests in the first half of June 8 days, in the second half of June 9 days, in July 13 days.

4. The 100 females that began to nest on 14 May produced 18 successful nests; mean brood size was 3.7 fledglings (Table 132). The 82 unsuccessful nests failed on 20 May (see preceding paragraph). Table 149 (p. 424) presents percentages of females that replaced nests at various dates. (The replacement rate per 5-day period fluctuated; I smoothed this curve.) About 94% of the 82 females replaced first nests without changing mates. Those that did not replace moved and probably obtained new mates (Chapters 30 and 31); mate-change is discussed in paragraph 6.

5. Mean replacement periods according to date appear in Table 36, mean times required to build in Table 49. Combining appropriate means for nests that failed 20 May and that were replaced determines date of laying in first replacement nests. Paragraphs 2 and 3, above, give the percentage of success of nests receiving eggs at that date as well as median active life of nests that failed. Brood size of those that succeeded, percentage of unsuccessful females that renested again, duration of the next replacement period and of building, etc., were obtained as before. With this information, rates (and dates, in case of failure) of second replacement nests were calculated, and this procedure was followed until dates extended beyond the end of breeding.

6. When females did not replace nests and left mates, males waited a mean 8 days before acquiring new females (pp. 96, 354), if any. I assumed females that left the study area after nest failure would pair 8 days later if still in breeding condition. Estimated proportions of females in breeding condition at various dates are given on page 423. I proceeded as in the following example: Suppose 10 females lost nests and left mates on 20 June; 8 days later probably only 50% of all females were still capable of breeding (p. 423); I therefore treated 5 of the 10 females as forming new pairs and nesting, 5 as having quit breeding. For the 5 new pairs, mean pairing-to-building period was 2 days (p. 116), which, added to mean duration of building for the date (Table 49), gave the date of laying egg 1. Successes, failures, and (if failures) active life of nests of these pairs were calculated as described above. However, females pairing in midseason replaced unsuccessful nests less persistently than females still mated to their original males (Table 151, p. 425); in calculating percentage of nest replacement by midseason pairs I halved the rates in Table 151.

7. Successful females attempted second broods at rates varying according to

date of nest-leaving by the first brood (Table 156, p. 430). The period from laying egg 1 to nest-leaving was usually 24–25 days, from nest-leaving to beginning the second-brood nest an average 10 days (p. 121). Percentages of females that attempted second broods and dates on which these laid egg 1 could therefore be calculated, as could success rates, brood sizes, and dates of failure. Females attempting second broods were less persistent in replacing nests than females whose first-brood nests failed; therefore after second-brood failures I halved the replacement rate applicable to first-brood nests.

8. With one exception, as the final step in each calculation I rounded to whole numbers; e.g. if mean replacement period plus mean duration of building totaled 6.6 days, I rounded to 7 days in fixing the date of egg 1. The exception was in calculating production of fledglings; fractional numbers of fledglings brought off by each group of females (e.g. the 18 whose first nests succeeded) were carried forward and the sum of these was rounded.

9. Polygyny was left out of the calculations; whether some hypothetical females shared a male with others should be irrelevant (see Chapter 31).

Simulation for the parasitized population used many of the same data but was complicated by the fact that when any group of females built nests some were and some were not parasitized. The result was many more subgroups, each requiring a separate calculation. Only steps not explained by, or differing from, those already described will be discussed.

1. Rates of parasitism are given on page 380.

2. Success (7%) of the 86 parasitized nests did not vary with date (p. 390), nor did median active life (4 days) of unsuccessful nests.

3. The 65 unparasitized first nests of the season had the same success rate and brood size as nests of the unparasitized population, of course. The 35 parasitized nests had fewer successes and smaller broods; failures had shorter active lives and were replaced (if replaced) at an earlier date. First replacement nests of unsuccessful females, regardless of whether their previous nests had been parasitized, were again exposed to parasitism, as was true of later replacement nests, at rates declining with date.

4. Combinations of successes and failures of groups and subgroups of females are illustrated by a flow diagram (Fig. 34), which for simplicity deals with only part of the population and fewer than all replacement nests. As a result of repeated subdividing, some groups of females became so small that pooling was necessary. As an example, if one or two females lost nests on 18 June and another female on 22 June, I pooled these cases for the next calculation. Often pooled cases fell within the same relevant calendar interval and no problem was presented by date-specific rates, means, etc. When pooled data crossed calendar lines and more than one rate became relevant, rates were averaged. Numbers of such cases were small and had no important effect on results.

5. The low success rate of parasitized nests caused a problem: application of 7% success to each small subgroup of nests parasitized in June would, if the results were rounded, always produce 0. I therefore pooled parasitized nests (28) from 9 dates in June and applied the 7% rate; this added 2 to the number of successful parasitized nests. The calculations described above are presented in detail in Appendix 4.

TABLE 133
SIMULATED AND OBSERVED REPRODUCTIVE SUCCESS^{1,2} OF PRAIRIE WARBLERS
EXPOSED AND UNEXPOSED TO COWBIRD PARASITISM

	Hypothetical unparasitized population	Hypothetical population exposed to parasitism	Observed territories ⁴
Females or territories ³	100	100	129
Nests			
Total built	333	360	400
Mean per female or territory	3.3	3.6	3.1
First-brood	311	343	— ⁵
Second-brood	22	17	— ⁵
Successful, N	66	62	89
Successful, %	19.8	17.2	22.3
% devoted to first- brood production	93.4	95.3	— ⁵
Production of young			
Total fledglings			
Prairie Warbler	226	196	278
Brown-headed Cowbird	0	5	4
Mean warbler fledglings per female or territory ³	2.26	1.96	2.16
Mean warbler fledglings per nest built	0.68	0.54	0.70
Mean warbler fledglings per successful nest	3.42	3.16	3.12
Total females or territories ³ producing 2 broods	5	5	13 (10%)
1 brood	56	52	63 (49%)
0 broods	39	43	53 (41%)
Nests built by individual females or on individual territories ³			
1 nest	4	3	14 (11%)
2 nests	22	19	29 (22%)
3 nests	32	23	44 (34%)
4 nests	24	28	23 (18%)
5 nests	17	24	13 (10%)
6 nests	1	3	4 (3%)
7 nests	0	0	1 (1%)
8 nests	0	0	0 (0%)
9 nests	0	0	1 (1%)

¹ Methods are described on pages 390–392; calculations are shown in Appendix 4.

² The sample is described in the text, this page.

³ Reasons for equating hypothetical production per female with observed production per territory are given on pages 419–420.

⁴ Some observed data are also shown as percentages to facilitate comparison with hypothetical populations.

⁵ For observed females, numbers that produced second broods are unknown; see text, this page.

Observed production—methods: The lack of a representative sample of season-long female histories complicates analysis of observed production (see discussion in Chapter 33), and I used full-season territory histories of 129 territories inspected daily. Data consist of numbers of nests, eggs laid, eggs hatched (see the sample 2 methods, p. 397), and young produced on these; pages 419–420 present reasons for believing that mean production per territory is equal to mean production per male and female.

Observed and simulated results cannot be compared with respect to extent and productiveness of the second-brood effort, because some observed females left or came to the study area in midseason (Chapter 30); therefore second-brood nests could not always be recognized as such.

Observed and simulated production of parasitized populations—results: Observed and hypothetical data are compared in Table 133. Observed production was 2.16 fledglings per territory, hypothetical production 1.96 fledglings per female. Although the calculated effort per female was somewhat greater than the observed (e.g. more nests built) and the success slightly less, I regard the differences as small and suggest that the simulation methods used will produce a useful estimate of the cowbird's impact on the Prairie Warbler.

Simulated production of parasitized and unparasitized populations—results: Speaking for the sake of simplicity as though reporting actual observations, the cowbird lowered the warbler's production by 13.3% (196 fledglings instead of 226; Table 133). This loss was produced as follows: (1) The parasitized population had 4 fewer nest successes, a 6.1% reduction. Persistent renesting and the difference in length of breeding seasons of warbler and cowbird did not quite compensate for the high failure rate of parasitized nests; 43 females in the parasitized group and 39 females in the unparasitized brought off no young. (2) Mean brood size of the parasitized population was smaller by 0.26 young, or 7.6%, because the six successful parasitized nests produced only 0.91 warbler each. (3) The parasitized population produced 30 fewer fledglings, despite its greater effort. Of its females, 55% built at least 4 nests, as opposed to 42% of females from the unparasitized population; and mean nests built, 3.6 per female, was 9.1% larger than the 3.3 per female in the unparasitized population. Such differences in effort could have long-term consequences on survival or reproduction of females, but that is speculation.

In sum, about 14 (47%) from the deficit of 30 fledglings produced by the hypothetical population arose because fewer nests succeeded and about 16 (53%) because in some nests that did succeed the presence of cowbirds reduced warbler brood size.

Additional calculations concerning the cowbird's effect on warbler production appear on page 412. Compare Hann 1937: 205; Hofslund 1957; Mayfield 1960: 177 and 181, 1965b; Friedmann 1963: 15–21; McGeen 1972.

REPRODUCTIVE SUCCESS OF COWBIRD

The sample, 102 cowbird eggs found on the day they were laid and observed daily thereafter, includes eggs laid in nests that had already failed. Table 134 shows probable causes of death of eggs and nestlings that did not survive. Certain categories require explanation. "Other cowbird's interference" includes four eggs that died after a female warbler had accepted them without deserting; death resulted (in one case, probably resulted) because a second cowbird subsequently laid and/or removed and/or broke egg(s). "Host desertion" includes all other desertions because of cowbird interference. Death because of "prior hatching of warbler eggs" occurred when a cowbird egg was laid after incubation had begun. Other terms are self-explanatory.

Survival.—Nine eggs (9%) of 102 laid survived to hatch and 5 (5%) to produce fledglings. The heavy mortality during the egg stage is typical (Young 1963b); host intolerance of interference and failure of the parasite to synchronize with host laying are major causes of death. Prairie Warblers evidently were fully

TABLE 134
CAUSES OF DEATH¹ OF COWBIRD EGGS AND NESTLINGS² IN PRAIRIE
WARBLER NESTS

Causes of death	Cowbirds dying			
	As eggs		As nestlings	
	N	% ³	N	% ³
Host desertion	45	46	0	0
Predation	36	37	4	4
Failure of nest prior to host laying	4	4	0	0
Other cowbird's interference	4	4	0	0
Embedding by host	2	2	0	0
Prior hatching of warbler eggs	1	1	0	0
Unknown	1	1	0	0
Totals	93	95	4	4

¹ Terms are defined on page 395.

² The sample is described on page 395.

³ Percents show proportion of all deaths per cause indicated. As rounded they do not total 100.

tolerant of cowbird nestlings (see Hamilton and Orians 1965: 367), which survived in higher proportions than host nestlings (compare Tables 131 and 134) for reasons already made clear.

The 5% success rate from parasitizing the Prairie Warbler is lower than percentages reported in most studies of cowbird relations with other hosts, as reviewed by Young (1963b), Friedmann (1963), and Mayfield (1965b); see also McGeen (1972). However, I question whether the rate is as unusual as Young's review would suggest; many papers from which he drew data used nests found at all stages of development, a method that Mayfield has discredited (see p. 378). For more than 20 years my students and I have inspected our study area almost daily. Studies of reproductive success of cowbird hosts, including the White-eyed Vireo, Bell's Vireo, Yellow-breasted Chat, Cardinal, Indigo Bunting, Field Sparrow and, on a smaller scale, several additional species indicate that the success rate of parasites of the Prairie Warbler was typical (see also Nolan 1963, Sutton 1960).

Causes of death.—Risks inherent in the parasitizing mode of reproduction caused the death of 52 cowbird eggs (51%; Table 134). Some were deserted simply because they were cowbird eggs, others probably because they were laid at inappropriate times. All parasite eggs, but of course only Prairie Warbler eggs in parasitized nests, were subject to dying because of dangers arising from brood parasitism. Therefore nest predation was a less important mortality factor for cowbirds (41%) than for warblers (79.6%; see Chapter 33), even though cowbird eggs faced all the dangers of predation and accident that host eggs did. As is usual, the cowbird's reproductive success was lower than its host's (see, e.g., Friedmann 1963: 15–21).

Probably 32 of 93 cowbird deaths (34%) at the egg stage resulted from faulty execution by parasitizing females. These cases consisted of 3 eggs laid during active building, 10 laid in nests in which cowbirds broke eggs, 15 subjected to interference during the incubation period, and 4 laid after nests had failed.

CHAPTER 33

REPRODUCTIVE SUCCESS AND RECRUITMENT FROM REPRODUCTION

NEST SUCCESSES AND FAILURES

Overall success rate.—Success and failure are defined on page 385. The terms are applied only to nests that were completed. Further, those that received no eggs and were abandoned apparently because of unfavorable weather (see pp. 185–186) are omitted from consideration, but those deserted apparently because of cowbird or predator interference are included as failures. Nest dates refer to the day egg 1 was laid or probably would have been laid. Active life is defined and calculated as described on pages 389–390.

Success varied with date, and season-long rates are based on years when field work was uninterruptedly and uniformly distributed throughout the season. Two samples are analyzed, sample 1 and sample 2; they overlap in part. Sample 1 consists of 400 nests built on 129 territories studied daily in the breeding seasons 1952–1966 (see also pp. 348–349); probably all nests were found, about 85% of them during active building. A few discovered after failure are included to avoid bias (see p. 378); therefore median and mean active life cannot be calculated for sample 1 nests. Sample 2 includes 300 nests (116 on the University Farm, 184 on the Griffey Tract) studied in the years 1952–1955 and 1958–1962, when special attention was given to nest observation; all were found before egg-laying began and observed daily. In both samples are a few high nests whose day-to-day situations were inferred from female behavior. Modal clutch sizes for the appropriate dates were attributed to these, and the 95% hatching rate (p. 407) was assumed for those that survived incubation. When nests failed on the day hatching was expected or was known to have begun, I assumed for high nests that half the clutch had hatched before the failure; for low nests, eggs that had been pipped when last inspected were assumed to have hatched, unpipped eggs to have succumbed before hatching.

In sample 1, 89 nests (22.3%) succeeded. One or more eggs probably hatched in 148 nests (37.0%); thus 60.1% of these 148 succeeded. About 1393 eggs were laid, of which about 521 (37.4%) hatched. The 278 fledglings produced amounted to about 20.0% of the eggs laid and about 53.4% of those that probably hatched. Four cowbird fledglings were brought off. Other data from this sample are reported below (pp. 418–420) and in Table 133.

In sample 2, 61 nests (20.3%) succeeded. That number is 56.5% of the 108 nests that survived until eggs hatched, which in turn is 36% of the 300 nests in the sample. About 1050 eggs were laid; about 366 (34.9%) hatched. These produced 194 fledglings, about 18.5% of the total laid and 53.0% of those that hatched. Also produced were five cowbirds. The median active life of nests was 10.1 days, the mean 11.4 days; the distribution of active lives was not normal (see pp. 402–404).

No difference between samples 1 and 2 approached significance.

TABLE 135
ACTIVE LIFE¹ OF NESTS² AND PERCENTAGE OF NEST SUCCESS,³ ACCORDING
TO DATE⁴

	Date				
	1-15 May	16-31 May	1-15 June	16-30 June	July
Nests	82	122	85	59	36
Active life in days					
Median	6.5	7.2	11.1	10.3	18.0
Mean	10.2	9.8	12.4	12.5	16.5
Cases below combined median ⁵	48	67	38	24	10
Nest successes					
N	12	15	15	13	13
%	15	12	18	22	36

¹ Active life is the number of days the nest was in use, counting the day egg 1 was laid as 1. See pages 389-390.

² The sample is described in the text, this page.

³ A nest was successful if it produced at least one fledgling Prairie Warbler or Brown-headed Cowbird.

⁴ Nests are assigned to the date on which egg 1 was laid or probably would have been laid had the nest not failed before laying began.

⁵ The combined median for all 384 nests is 9.6 days.

Variation according to date.—Success varied with date. Analysis is based on nests found during active building and inspected daily and is not limited to nests from years in which fieldwork was evenly distributed through the season. Nests are grouped by half-months, except that all July nests are pooled.

As shown (Table 135), 15% of nests in the first half of May succeeded; the median active life was 6.5 days. These rates changed little in the second half of May but rose to 18% in early June and 22% in late June; median active life in June was considerably higher than in May (11.1 days in early June). For July nests, success was 36% and median active life 18.0 days. In a test of independence of successes and failures per half-month period Chi-square = 12.3; df = 4; $P < 0.02$. When active lives are tested by extension of the median test (see Table 135, footnote 5) the result is similar: Chi-square = 11.7; df = 4; $P < 0.025$. My conclusion that Prairie Warbler nests were progressively more successful from early June onward is reinforced by published (Nolan 1963, Thompson and Nolan 1973: 159-160) and extensive unpublished observations of a similar change in success of various other species on the study area.

An increase in success in June and July is reflected in dates at which broods left the 61 successful nests in sample 2: 2 left in May, 18 in the first half of June and 11 in the second, 12 in the first half of July and 14 in the second, 4 in August. The median date of nest-leaving was 30 June, the mean 7 July, the extremes 25 May and 15 August. Recalling that 24-25 days usually elapsed between laying of egg 1 and nest-leaving and that about 60% of all Prairie Warbler nests were built in May (e.g. see Table 46), it is revealing that 30 of 61 successes were as late as July and August. These data raise the question why selection has not shifted breeding later into the summer. Part of the answer may be the bigger clutches and larger broods (Chapter 18 and this chapter) of early nests, larger presumably because parents can provide more food for early broods (see Lack 1966: 273). Also, a higher proportion of early fledglings may survive to reproductive age, as reported in several species (e.g. Löhrl 1957: 163-168, Collared Flycatcher; Perrins 1963, 1965: 621-622, Great Tit; Lack 1966:

TABLE 136
SUCCESS¹ AND ACTIVE LIFE² OF NESTS,³ ACCORDING TO DATE⁴ AND HEIGHT

Height	Date				
	1-15 May	16-31 May	1-15 June	16-30 June	July
0-1 m					
Nests	22	22	13	7	1
Nests this height as % of all nests in period	35	26	22	18	4
Successful nests					
N	7	2	2	0	0
%	32	9	15	0	0
Active life					
Median	11.5	6.5	6.7	3.3	—
Mean	13.1	11.1	9.2	5.1	—
1-2 m					
Nests	32	43	27	16	9
Nests this height as % of all nests in period	52	51	46	40	39
Successful nests					
N	4	1	2	2	2
%	13	2	7	13	22
Active life					
Median	4.8	5.4	10.7	11.0	14.8
Mean	8.2	8.0	11.3	11.8	15.1
2 m and above					
Nests	8	19	19	17	13
Nests this height as % of all nests in period	13	23	32	43	57
Successful nests					
N	0	0	4	6	5
%	0	0	21	35	38
Active life					
Median	4.5	8.0	11.8	9.0	10.0
Mean	5.9	8.8	11.2	14.3	14.4

¹ A nest was successful if it produced at least one fledgling Prairie Warbler or Brown-headed Cowbird.

² Active life is the number of days a nest was in use, counting the day egg 1 was laid as 1. See further pages 389-390.

³ The sample is described in the text, this page.

⁴ Nests are assigned to the date on which egg 1 was laid or probably would have been laid had the nest not failed before laying began.

259-260, Manx Shearwater; see also Murton *et al.* 1974: 52). Two few Prairie Warblers showed hatching-site fidelity to permit a test of this hypothesis. Another possible factor selecting against delayed breeding is that adult survival might suffer; postponement would require rescheduling of other events and processes and might be especially costly to an insectivore that must make the Prairie Warbler's long migration.

Variation according to nest height.—Success varied according to nest height, the relationships also shifting with date. Analysis is based on half-month periods. Heights are classed as low (0-1 m), medium (1-2 m), and high (2 m and above). The sample (Table 136) is 268 nests from the Griffey Tract, all of them included in the analysis of variation according to date, above. Heights of these 268 are representative of heights of all Griffey nests during the study (compare Table 136 with Table 42).

Frequency of low nests decreased from 35% to 4% between early May and

TABLE 137
SUCCESS¹ AND ACTIVE LIFE² OF NESTS,³ ACCORDING TO YEAR AND SECTION
OF STUDY AREA⁴

Year	Section of study area ⁴	Total nests	Successful nests		Active life of nests, days	
			N	%	Median	Mean
1952	U.F.	40	14	35	19.0	15.6
1953	U.F.	31	8	26	16.8	14.7
1954	U.F.	33	5	15	9.8	12.0
1958	G.T.	32	5	16	8.5	11.0
1959	G.T.	34	7	21	8.5	11.6
1960	G.T.	36	7	19	7.5	10.3
1961	G.T.	52	6	12	6.7	9.3
1962	G.T.	30	4	13	9.5	11.4

¹ A nest was successful if it produced at least one fledgling Prairie Warbler or Brown-headed Cowbird.

² Active life is the number of days a nest was in use, counting the day egg 1 was laid as 1. See further pages 389-390.

³ The sample is described on page 401.

⁴ See introduction. U.F. is the University Farm, G.T. the Griffey Tract.

July and high nests increased from 13% to 57% (see Table 136). Accompanying this shift was a change in probability of success at the various heights: In early May low nests succeeded at a 35% rate, high nests at 13%; median active life of low nests was 11.5 days, of high nests 4.5 days. By late June-July this success: height relationship was approximately reversed. Nests of medium height, the most numerous class over the season as a whole, showed less clear trends. For example, their proportion decreased slowly as high nests became more numerous, although their median active life was improving. Such anomalies might disappear if the sample were enlarged and height divided into smaller unit intervals.

With the data subdivided into as many as 15 classes, as in Table 136, statistical tests of variation in success (1) by height within the same period and also (2) by period within the same height interval produce few significant values (Chi-square, extension of median, Kruskal-Wallis one-way analysis of variance). However, the trends in Table 136 are clear: (1) Height had an important bearing on chances of success; (2) optimum height gradually shifted upward; and (3) proportion of nests per height interval shifted in parallel with increasing probability of success at that interval.

Judging from the very few high nests built before 16 May and few low nests built after 15 June as well as from the poor success of both these groups, pressures affecting nest height may have been most intense early and again late in the breeding season. Early nests, built when concealing vegetation was least developed, probably were less likely to be discovered if placed near the ground. Note the suggestive evidence (pp. 380-381) that cowbirds laid in high nests more frequently than in low; see also discussions of the conspicuousness of early high nests (Chapter 15) and the relationship between conspicuousness and success (p. 401).

Seasonal changes in microclimate and exposure to weather may also have affected nest placement, with predation pressure perhaps primarily responsible for heights of early nests and climatic or other factors more important later. Also, the increased success of later nests may have been wholly or partly unrelated to height changes; for example, in July cowbirds (Chapter 32) and snakes (pp. 413-415) were less serious threats to nests, whatever their heights.

Annual differences and differences between locations.—Annual differences and factors associated with the sections of the study area probably affected nest success independently. However, data on the two points are presented together (Table 137), because no substantial amount of field work was carried out on both University Farm and Griffey Tract in the same year(s). The nests in Table 137 are those of sample 2, excluding nests from 1955 because of their small number.

Of 103 University Farm nests, 27 (26%) succeeded, compared to 29 (16%) of 184 nests at Griffey; adj. Chi-square = 4.0; $df = 1$; $P < 0.05$. The median active life of all 287 nests combined was 9.8 days, of University Farm nests 14.8 days, and of Griffey nests 8.5 days; in a median test, adj. Chi-square = 7.9; $df = 1$; $P \approx 0.005$. The highest (most successful) annual median active life at Griffey was lower (worse) than the lowest (least successful) at the University Farm, and two annual medians from the University Farm greatly exceeded any from Griffey. It therefore seems probable that the statistical difference was not wholly due to annual variation. Nest placement differed between tracts in ways consistent with vegetational (and not annual weather) differences (Chapter 15), making a sectional difference in success even more likely.

Extreme annual success rates were 35% and 12% (Table 137), extreme median active lives 19.0 and 6.7 days; 1952 and 1961 were the extreme years. However, when the annual data for each tract are tested separately to eliminate variation associated with location, results are nonsignificant (Chi-square, extension of median, Kruskal-Wallis one-way analysis of variance). Despite this I suspect annual variation, for the following reasons: (1) Cowbird parasitism probably varied annually (Chapter 32). (2) Spring weather (e.g. late frosts) varied greatly from year to year and affected nest concealment and therefore success; see the next subsection for a probable relationship between concealment and success. (3) Date of end of nesting appeared to vary annually (Chapter 34); early termination of breeding prevented females from benefitting by the high success rate in July, thus lowering the annual rate (compare Thompson and Nolan 1973: 164). For example, 1954 produced the poorest success on the University Farm and nesting ended earliest in that year (Table 152); in 1952, the most successful year, nesting ended latest. (4) Numbers of snakes and chipmunks, major nest predators (below), may have varied annually. Fluctuations in rodent populations are well known, and Klimstra (1958: 236) found that "striking yearling variations in [snake] numbers were not uncommon."

Variation according to concealment.—I evaluated concealment as either below average or average and above on the basis of difficulty that I had in finding nests or probably would have had (in cases in which female behavior revealed locations and made searching unnecessary). To the extent that nest predators relied on vision, conspicuousness of nests to me might be correlated with conspicuousness to them.

Of 33 Griffey nests 1–2 m high whose concealment was below average, none was successful; 42 Griffey nests at the same height but average or above in concealment produced 9 (21%) successes ($P < 0.02$). The median active life of the poorly concealed nests was 5.3 days; of average or above, 11.5 days; of the combined nests, 9.2 days. In a median test, adj. Chi-square = 4.1; $df = 1$; $P < 0.05$. (Compare Nice 1937: 93–94.)

TABLE 138
RATE OF NEST FAILURE¹ EARLY AND LATE IN BREEDING SEASON,²
ACCORDING TO STAGE OF NEST³

Stage of nest cycle	Early nests			Late nests		
	Inspections N	Nest failures discovered		Inspections N	Nest failures discovered	
		N	%		N	%
Inactive building ⁴	320	6	2	44	1	2
Day of laying ⁵						
1	153	3	2	54	1	2
2	156	13	8	57	3	5
3	145	21	15	—	—	—
Final	120	18	15	78	6	8
Day of incubation						
2-3	181	10	6	88	2	2
4-5	156	9	6	83	5	6
6-7	142	9	6	73	6	8
8-9	125	13	10	68	3	4
10-11	108	8	7	67	6	9
Hatching day	60	9	15	28	3	11
Day of nestling interval						
2-3	83	8	10	50	0	0
4-5	71	4	6	53	2	4
6-7	64	4	6	56	3	5
8-end	81	9	11	59	4	7

¹ A nest failed if it did not produce at least one fledgling Prairie Warbler or Brown-headed Cowbird.

² The early sample includes nests that received egg 1 in May or probably would have done so had eggs been laid. The late sample includes nests that received egg 1 on or after 21 June or probably would have done so had eggs been laid. All nests were on the Griffey Tract.

³ See pages 402-403 for a description of methods used in pooling data.

⁴ This term is defined on page 149.

⁵ See page 199.

Variation according to stage of nesting cycle.—Success varied according to stage of reproduction. Because of seasonal changes in success, analysis is of an early (egg 1 laid in May) and a late (egg 1 between 21 June and end of breeding) sample, both from Griffey. Neither success rate nor rate of cowbird interference varied in May; these rates were not constant after 21 June, but the variation cannot be avoided. Any nest observed on 2 or more successive days is included if age of its eggs and/or young was known; such observations provide data on daily rates of failure between a nest's discovery and its success or failure (see Mayfield 1961). As a check on rates calculated from this sample I determined daily rates of failure using only nests found before laying began. No differences were suggested, and the latter are not presented.

When hatching was due, I usually visited a nest early and again later in the day and therefore know the day of failure of many nests at that stage. Most other failures fell between inspections on different days, and these I arbitrarily assigned to the day I discovered them (compare pp. 389-390). Where daily rates appeared to fluctuate randomly I pooled data and calculated a daily mean for the days involved. This procedure also eliminated problems caused by variation in length of certain stages of the cycle. Days for which data were pooled are (1) inactive phase of building; (2) days 3 and 4 of laying in early nests with 5 eggs; (3) days 2 and 3 of laying in late nests with 4 eggs; (4) each 2 days of the in-

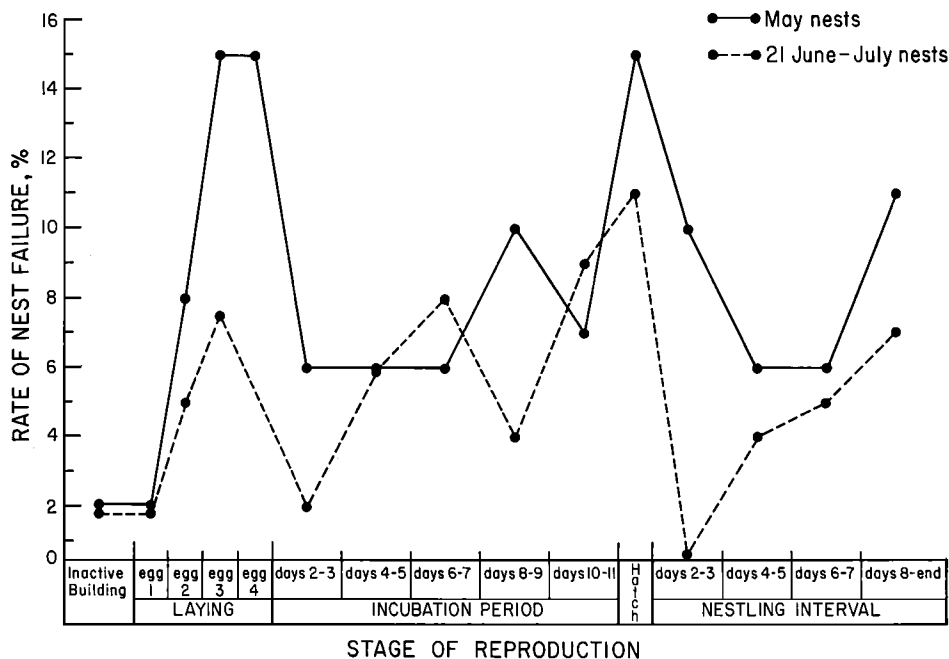


FIGURE 35. Rates of failure of nests built 1-31 May and 21 June-July, according to stage of reproduction. See Table 138 and text.

cubation period, from day 2 through day 11; and (5) each 2 days of the nestling interval from day 2 through day 7. The last part of the incubation period and nestling interval were treated specially: When hatching did not begin on day 12 of incubation, data from day 12 were added to the pooled data from days 10 and 11. All data from day 9 of the nestling interval through the day on which the young left or died were pooled.

Figure 35, based on Table 138, graphs the fluctuations in daily rate; for a survival curve see Chapter 38. Shapes of the curves for early and late nests are fairly similar and suggest the following summary: Losses were fewest before laying of egg 2, then rose sharply on the day of egg 2 and again next day; in May nests, in which at least 4 eggs were usual (Table 54), the rate remained high on the day of egg 4. A sharp decrease coincided with the end of laying, after which the rate probably remained constant until hatching day. (Note the negligible fluctuation between incubation days 2 and 7 at early nests. Although the graph shows changes in rate late in incubation at May nests, the opposite changes occurred late in incubation at late nests; this suggests that both changes are products of sampling error. Adult behavior and appearance of the nest do not change during incubation in ways that might cause failure rates to vary.) Hatching day was a second point of maximum danger, followed by a brief decline to about the incubation-period rate. Failures began to increase on days 5 and 6 of the nestling interval and reached a third peak at its end. The following paragraphs suggest explanations for the higher loss rates at certain stages.

1. Laying interval.—Even with elimination of cowbird-caused desertions, which

in May were a major source of failure (Chapter 32), losses during laying were higher than during incubation. (a) Females were more prone to desert when disturbed by me, and therefore probably when disturbed by predators, during the laying interval than thereafter. Rates of desertion following my netting of females at or near the nest were 5 of 10 birds during building, 3 of 10 birds on the days of laying egg 1 through the next-to-last egg, 5 of 7 birds on the day of laying the final egg, 1 of 19 birds between day 2 of incubation and hatching day, and none of 37 birds after hatching day (or after I had introduced young into nests, which I did to insure against desertion). (b) Predators searching randomly would probably discover conspicuous nests in greater numbers (and also sooner) than concealed nests; if discoveries of inconspicuous nests were more evenly distributed over the cycle, a peak of early failures would be expected (compare Willis 1973). As a possible test of this hypothesis I scattered marbles over a large area, hiding some well and leaving others conspicuous; members of my family searching randomly at a steady pace found many marbles in the first several minutes, smaller and approximately equal numbers per minute thereafter. Cowbirds after discovering nests under construction sometimes return to them until the appropriate time for parasitizing (Mayfield 1960: 164–171), and some predators might possibly do the same. If so, the potential for predation may accumulate before eggs are laid, resulting in many failures as soon as laying begins. Snakes (p. 413), chipmunks (p. 415), and Blue Jays (p. 416) return to nests from which they previously have taken part of the contents, demonstrating their ability to remember and come back to such nests. Therefore it seems likely that some, finding an empty nest, may remember it and return if doing so is rewarded sufficiently often. Eggs may be more conspicuous to avian predators during the laying interval, when they are uncovered most of the time.

2. Hatching day.—Increased losses on hatching day may result from changes in adult behavior (e.g. see Fig. 25). Evidence that food-bringing may attract predators is that some adults appeared to behave cryptically when going to the nest (p. 276). This suggestion leaves unexplained the reduction of failures early in the nestling interval.

3. Nestling interval.—The failure rate might be expected to climb as feeding trips become more frequent and conspicuous. The sharp rise in losses late in the interval I attribute to noisiness of some broods at that time (p. 300; compare Perrins 1965: 616) and to the adults' much more frequent feeding trips (Chapter 24).

Success and age of female.—Of 107 nests, each the first built by a female during a particular breeding season, 73 were constructed by old birds and 34 by yearlings. Success rates did not differ between these groups (10% success for old females, 9% for yearlings), and median active lives were the same.

Effects of activities of the investigator.—I avoided touching nests after the eggs were marked, staying away from them when possible (e.g. when the female's presence indicated that they had not failed) and often walking to various trees nearby to leave less direct and possibly less easily followed trails; some nests, including all that were high, I avoided entirely, examining them daily from a distance. For the following reasons I conclude that the investigation did not reduce the

success rate or length of active life: (1) I approached low nests most closely. If predators followed my scent, they should have found these most readily. Yet during much of the season low nests had the highest success; conceivably success might have been even greater if I had not inspected them at all, but the regular trends in Table 136 do not suggest an artifact of the study. Nests above 4–5 m could not be approached at all, but they succeeded in about the same proportions as nests 3 m high, which I often approached. Low nests that I studied in greatest detail and visited most often were as successful as low nests that I intentionally avoided. (2) Two major causes of nest failure, cowbirds and Blue Jays, do not discover nests by olfaction, and it is difficult to believe they used my many intersecting paths as visual clues. Similarly, although olfaction of snakes (Parker 1965:22) and chipmunks is acute, I left so many trails that these animals would have received few rewards by following human scent to trees (compare Stoddard 1932: 195). (3) In 1974 colleagues and I studied Cardinals and Indigo Buntings on a large tract of which the Prairie Warbler study area was part. Some 15–18 male Prairie Warblers held territories there; we saw their nests but did not approach or investigate them in any way. By 31 July, after daily field work and almost daily mist netting of the area, we had not seen, heard, or caught a fledgling Prairie Warbler; it is certain that few or none had been produced on the tract. (4) In experiments in shrub habitat in Ohio, Charles Thompson and B. Gottfried placed passerine nests and *Coturnix* eggs in small trees, half of which were inspected daily and half weekly. Results to date show no greater predation of nests visited daily (pers. comm.).

The view that my fieldwork did not affect reproductive success is reinforced by similar conclusions of Coulson (1958) after study of the Meadow Pipit; Stoddard (1932: 195), the Bobwhite; Allen (1938: 417), several species; and Willis (1973), the Bicolored Antbird.

Success and population density; spacing of nests.—Nest density varied in parallel with population density. Ricklefs (1969: 25–26) has discussed evidence that increasing nest density causes greater mortality of eggs and young; see also Krebs (1971: 16–17). Comparison of annual rates of nest success (Table 137) and changes in population density (see Chapter 38) indicates that rate of success and density of Prairie Warblers probably were not associated.

EGG AND NESTLING DEATHS NOT ATTRIBUTABLE TO COWBIRD

Methods.—This section deals with piecemeal or within-brood losses, i.e. disappearances and/or deaths of fewer than all contents of nests that continued in use (see Ricklefs 1969: 3, 8–9). It excludes cases associated with cowbird interference, the subject of Chapter 32, and divides all other piecemeal deaths and losses into egg disappearance prior to hatching day, failure to hatch of eggs that did not disappear, disappearance of eggs and nestlings on hatching day, and disappearance or death of nestlings.

A few young died or disappeared at about the age of nest-leaving. These cases were treated as nestling rather than fledgling deaths, if siblings remained in the nest beyond the day on which a bird disappeared and circumstances indicated

that the dead bird had not left under its power or that it had been stimulated to leave prematurely (by bites of ants).

The sample includes nests found at whatever stage, provided the stage was known and inspections were made every 24 hours thereafter, thus producing information on daily rates of loss. Preliminary segregation of nests according to date gave no evidence of seasonal variation, and data from all dates are pooled. Similarly no variation according to location was detected, and results from the University Farm and the Griffey Tract are combined.

Disappearance of eggs: The egg-disappearance rate varied during laying. Observations are presented separately for each day beginning with day 2, i.e. with the inspection that could disclose a disappearance following laying of egg 1. The laying interval is regarded as lasting 4 days to correspond to the modal clutch size, and data for 3- and 5-egg clutches are treated as described on pages 199, 381. Between laying of the final egg and nightfall of the day before hatching day, rates of egg disappearance did not appear to vary; therefore all observations for the incubation period were pooled and a mean daily rate obtained.

If a nest was parasitized by the cowbird, all disappearances during the laying interval were ascribed to the parasite and were omitted from the analysis; disappearances during the incubation period were ascribed to the cowbird only if they occurred within 1 day of the cowbird's laying. Parasitized nests that the warbler did not desert remained vulnerable to piecemeal egg loss and were retained in the sample. No distinction was drawn between disappearance of cowbird and host eggs.

Hatching rate; brood size at hatching: Methods of determining hatching rate are described on page 385. Only nests that never held cowbird eggs were considered. There are 2 samples: 64 nests inspected daily from building until end of hatching, and 104 nests (40 in addition to those just referred to) found anytime before hatching and observed throughout the hatching interval. For the latter, the approximate number of eggs laid but not producing nestlings can be obtained by assuming the 40 clutches were of mean size for their dates (see Table 54), then subtracting the number of eggs that hatched. Dates of laying in nests of both samples are representative of dates for all nests in which eggs hatched.

Disappearance on hatching day: When nest contents decreased between inspections on hatching day, I assumed that the missing animal(s) disappeared after hatching unless (two cases) I found them, still eggs, beneath the nest.

Disappearance and death after hatching day: Analysis was limited to nests that never held cowbird and Prairie Warbler nestlings simultaneously. Nestling disappearance rates varied and are presented separately for each day. When only one nestling remained (two cases), further piecemeal disappearance was impossible and nests were dropped from the sample.

Results.—Disappearance of eggs: Overall loss: The 64 nests observed from laying through the day preceding hatching day received 245 eggs; 6 lost 1 egg and 1 lost 2. Thus 11% of these nests lost 3% of all eggs laid. Variation according to clutch size was not apparent. Loss before hatching can also be calculated from daily rates of disappearance (Table 139) applied to constantly changing egg numbers in 100 hypothetical nests. If 389 eggs were laid (based on mean clutch size;

TABLE 139
DISAPPEARANCE OF EGGS FROM NESTS THAT REMAINED ACTIVE,¹ ACCORDING
TO STAGE OF NESTING PRIOR TO HATCHING DAY

Stage	Observations ²	Eggs expected ³	Eggs observed	Eggs disappearing		Nests from which eggs disappeared	
				N	%	N	%
Laying interval ⁴							
Day 2	302	604	578	26	4.3	20	6.6
Day 3	280	816	806	10	1.2	10	3.6
Final day	231	896	892	4	0.5	4	1.7
Incubation period ⁵							
Day 2 to day preceding hatching	1565	5876	5846	31	0.5	27	1.7

¹ Disappearances associated with laying of cowbird eggs are excluded. Sample and methods are described on page 406.

² Disappearances fell during roughly 24-hour intervals between inspections; number of observations indicates pairs of observations, the later of which was at the stage shown.

³ The expected number is the number that would have been present had no eggs disappeared since the preceding inspection.

⁴ The day of laying egg 1 is not shown; no eggs had been present preceding that day. Treatment of clutches of 3 and 5 eggs is described on page 199.

⁵ Daily rates appeared not to vary, and data for these days are pooled.

see Table 54), 19 would disappear assuming the daily disappearance rates in Table 139, for a 5% loss. Given the larger sample from which the daily disappearance rates are calculated, 5% is probably a better estimate than 3%.

Daily losses: Disappearance rate was highest on the day egg 2 was laid. Seven percent of all nests had lost one or both of the eggs expected when I visited them that day; 96% of the expected eggs were present. A sharp decrease in disappearance followed on day 3 and another on the final day of laying, when the rate became the one that prevailed throughout incubation. This distribution of egg losses conforms rather closely to the distribution of nest failures prior to hatching day (Table 138). The similarity is to be expected, since both piecemeal and total failures were very largely attributable to predators (pp. 411–412); in fact, significant numbers of nest failures resulted from desertion after fewer than all eggs had disappeared (Table 140).

Hatching rate of eggs; brood size at hatching: Unparasitized nests observed throughout the hatching interval numbered 99 and contained 372 eggs at that time; 19 (5.1%) from 18 nests failed to hatch (compare Mayfield 1960: 195, Thompson and Nolan 1973: 161). The rate did not vary with date or between nests that held three and four eggs: Of 25 nests with three eggs, in 5 (20%) one egg failed to hatch; of 70 nests with 4 eggs, in 11 (16%) one egg and in 1 (1%) two eggs failed to hatch. Clutches of other sizes (as of hatching, not laying) were too few to yield information.

Of the 64 unparasitized nests observed from laying through hatching, 4 received 5 eggs, 46 received 4 eggs, 13 received 3 eggs, and 1 received 2 eggs, for a total of 245 eggs. Eight of these did not hatch, and 12 others disappeared; thus 8.2% did not produce nestlings. Eighteen (28%) of the 64 nests produced nestlings from fewer than all eggs laid; losses were randomly distributed with respect to original clutch size. Mean number of eggs hatched per nest was 3.52 (SD 0.71).

Among the 104 nests observed throughout the hatching interval, 5 eggs hatched

TABLE 140
CONDITION OF NEST FOLLOWING FAILURES¹ PROBABLY CAUSED BY PREDATORS²

Condition of nest	Cases	
	N	%
Nest intact:		
All contents missing (total 153, or 61%)		
Failed before hatching began	108	43
Failed after hatching began	45	18
Part of contents missing (total 53, or 21%)		
Failed before hatching began, only unbroken egg(s) remaining	37	15
Failed before hatching began, egg shells or shells and unbroken egg(s) remaining	10	4
Failed after hatching began, all nestlings missing but unbroken egg(s) remaining	5	2
Failed after hatching began, dead nestling(s) remaining	1	1
All eggs present, female killed ³ (total 2, or 1%)	2	1
Nest demolished or damaged:		
All contents missing (total 39, or 16%)		
Failed before hatching began	32	13
Failed after hatching began	7	3
Part of contents missing		
Egg or eggs remaining (total 3, or 1%)	3	1
Total	250	100

¹ The sample is described on page 406.

² All losses not caused by the Brown-headed Cowbird, by weather, or by ectoparasites are attributed to predators.

³ Feathers were found around the nest.

in 3, 4 eggs in 59, 3 eggs in 34, and 2 eggs in 8, for a total of 369 nestlings. Mean brood size at hatching was 3.55 (SD 0.46). If original clutches are assumed to have been of mean size (3.89), mean reduction at the end of hatching was 0.34 eggs, and the calculated number of eggs that died before hatching amounts to 8.8%.

Disappearance on hatching day: Of 90 nests inspected on hatching day, 1 lost 2 nestlings and 6 lost 1 egg or 1 nestling (total 2 eggs, 6 nestlings). This represents 2.6% of the contents that had been present at my first inspection that day. For other details, see Table 141. Two egg losses occurred after nest-mates had hatched; the missing eggs lay intact below the nests, one of them pipped. The days were windless. Adult warblers were never known to remove eggs, and it is likely that activity of the females, i.e. picking at eggs or tugging at young, ejected these two eggs.

Disappearance and death after hatching day: Overall loss: Of 55 nests inspected throughout the nestling interval, 11 (20%) lost nestling(s); 14 (7.3%) of 192 birds that hatched disappeared or were found dead in the nest. A second estimate of overall piecemeal nestling loss is based on calculations from the daily rates (Table 141; see p. 409): If in 100 unparasitized nests mean eggs hatched numbered 3.55 (above) and hatching-day losses were 2.6%, 346 nestlings would be present on day 2. At nest-leaving, 304 birds would remain, a 12.1% loss. The considerable difference between the 7.3% observed loss and the 12.1% calculated loss prompts a third estimate: If mean brood size after

TABLE 141
DISAPPEARANCE¹ AND DEATH OF EGGS² AND NESTLINGS FROM NESTS THAT
REMAINED ACTIVE, HATCHING DAY UNTIL NEST-LEAVING

Day	Observations ³	Nestlings expected ⁴	Nestlings observed ⁴	Nestlings ² disappearing		Nests from which nestlings disappeared	
				N	%	N	%
Hatching day	90	311	303	8	2.6	7	7.8
Day 2	86	299	287	12	4.0	10	11.6
Day 3	83	280	271	9	3.2	8	9.6
Day 4	79	264	261	3	1.1	1	1.3
Day 5	77	254	253	1	0.4	1	1.3
Day 6	75	247	243	4	1.6	4	5.3
Day 7	70	229	225	4	1.8	3	4.3
Day 8	66	212	211	1	0.5	1	1.5
Day 9	60	193	193	0	0.0	0	0.0
Totals	686	2289	2247	42	1.83 ⁵	35	5.10 ⁵

¹ See page 406 for methods.

² Two eggs disappeared on hatching day; all other deaths and disappearances were of nestlings.

³ Disappearances fell during roughly 24-hour intervals between inspections; therefore number of observations indicates pairs of observations, the later of which was on the day shown.

⁴ Expected number is the number that would have been present had no eggs or young disappeared since the preceding inspection.

⁵ These rates are calculated from total observations and total disappearances.

hatching was 3.55 and a mean 3.36 fledglings left unparasitized successful nests (Table 132), the loss is 5.4% of the number present on hatching day. The 3 estimates indicate that 5–12% of nestlings disappeared from successful nests, with a figure near the lower extreme indicated by 2 of the methods.

The 55 nests inspected throughout the nestling interval suggested that disappearances were more frequent from the larger broods: 3 young disappeared from 1 of 2 nests containing 5 nestlings (apparently because the nest gradually and drastically tilted as the young grew). Of nests containing 4 young the day after hatching, 6 lost one nestling and 1 lost 2 (24% of 29 nests). Among broods of 3, each of 3 nests (17% of 18 nests) lost 1. No nestlings were lost from six broods of two. Disappearances did not vary according to date.

Daily losses: Of 34 disappearances after hatching day 21 (62%) fell on days 2 and 3 of the nestling interval (Table 141). If data for hatching day are included, 69% of all piecemeal deaths occurred during about 2.5 days, beginning when the first egg hatched (compare Mayfield 1960: 195). A decrease on days 4 and 5 probably was followed by an increase on days 6 and 7. At the very end of the interval within-brood losses were absent, although nest failures were numerous (Table 138).

The high disappearance rate on hatching day and days 2–3 probably was caused by falling of eggs from the nest on hatching day and occasional preferential predation on nestlings, leaving unhatched eggs (see p. 388 and Table 140). Speculative additional causes are greater vulnerability of very young nestlings to adverse environmental conditions and disease. By days 4 and 5 all or nearly all disappearances probably resulted from predation. Some losses on days 6 and 7 were caused by falls from nests sagging under heavier loads. Further, four nestlings of this age (in three nests) gradually lost normal reddish skin color and became yellowish, then died. Suspecting that blowflies (*Protocalliphora*) might be responsible, I examined the nests and found maggots in them. Also, at this

TABLE 142
NUMBER OF FLEDGLING¹ PRAIRIE WARBLERS PRODUCED BY SUCCESSFUL
NESTS,² ACCORDING TO DATE³

Fledglings in brood	1-15 May	16-31 May	1-15 June	16-30 June	July	Total broods
1	0	2	1	1	0	4
2	1	6	3	4	4	18
3	6	2	7	10	12	37
4	10	9	7	5	3	34
5	1	0	0	0	0	1
Total broods	18	19	18	20	19	94
Mean	3.6	2.9	3.1	3.0	2.9	3.11
SD	0.7	1.1	0.9	0.8	0.6	0.87
Median	3.7	3.3	3.2	3.0	3.0	3.18

¹ A fledgling left the nest at the end of a normal nestling interval (see Chapter 27).

² The sample consists of 76 nests that were not parasitized by the Brown-headed Cowbird, 6 nests that were parasitized and that produced at least 1 Prairie Warbler, and 12 nests in which there were no cowbirds at times of discovery and nest-leaving. Cowbird fledglings are not counted.

³ Nests are assigned to the date on which egg 1 was laid.

time some individuals may have jumped from the nest when irritated by ants (p. 417). The absence of within-brood disappearances at the very end of the interval is probably explained by the fact that when one nestling left or was taken from the nest at this age, the whole brood left it (see pp. 305-306).

Comparison of egg and nestling losses.—Egg disappearances per day were fewer than nestling disappearances (compare Table 139 and 141), but parents removed dead nestlings and not dead eggs. Combining disappearances of eggs with failure to hatch, rates of egg loss (8-9%) and of nestling loss (6-12%) were about the same.

SIZE OF BROODS LEAVING SUCCESSFUL NESTS

The sample is 94 nests, 76 never parasitized, 6 parasitized, and 12 containing no cowbird egg or cowbird when found (see p. 389). Brood sizes at nest-leaving are shown for the season as a whole and also according to half-month periods based on egg 1 date (Table 142).

For the season, mean brood size was 3.11 warblers; 3 and 4 were about equally the modal numbers. The largest half-monthly mean (3.6) was produced by nests receiving egg 1 before 16 May, when clutches were largest. Mean sizes for the four subsequent periods did not vary (2.9-3.1), although the mean clutch laid probably decreased in each half-month (Table 54). The seasonal decline in within-brood losses from cowbird parasitism probably counteracted the decrease in clutch size (see Chapter 32).

RELATIVE IMPORTANCE OF WHOLE-BROOD AND WITHIN-BROOD LOSSES

Ricklefs (1969) has determined for various species the proportions of egg and nestling mortality caused by nest failure and by piecemeal loss. The following is an estimate for a hypothetical Prairie Warbler population breeding under the conditions of my study area. Overall nest success is taken as 21%, from sample 1 and 2 rates on page 397. If 1000 nests held 3888 eggs (Table 54) and 790

nests failed, 3072 eggs and young would die. (The relatively few piecemeal losses prior to failure are ignored.) In the 210 successful nests, mean clutch laid, 3.89, would be reduced to 3.11 fledglings, with 163 piecemeal losses. Of the total 3235 deaths, 95% would be attributable to nest failure, 5% to partial loss.

COWBIRD-CAUSED NEST FAILURES

Causes of nest failure have first been separated into cowbird interference and all other hazards. Cowbird-caused losses were so differently distributed over the nesting cycle that different standards for selecting samples are required. For this reason and because of the many dimensions of the subject of warbler-cowbird relations, these losses are treated in Chapter 32. However, this section presents the proportion of cowbird-caused failures and nestling deaths and analyzes the timing of these. The sample is drawn from the 336 nests used to determine frequency of cowbird parasitism (pp. 378–379) and consists of the 246 of these that failed for whatever reason.

Two criteria identify failures as caused by cowbirds: (1) the nests were parasitized, and (2) the female warblers deserted either immediately or, if they laid after interference, before incubating.

Of the 246 failures, 44 (17.9%) were attributable to cowbirds. Among 156 failures in May (egg 1 date or projected date if the host laid no egg), 37 (24%) were due to cowbirds. Between 1 June and 20 June, 7 (12%) of 59 failures were caused by cowbirds, and thereafter none of 31 failures. No cowbird-caused failure occurred later than the 13th day of active life, and 36 (82%) were no later than the 4th day. Median active life of the 44 nests that cowbirds caused to fail was 2.9 days, of the 202 nests that failed for other reasons 8.2 days; in a median test, $P < 0.01$.

To learn whether parasitism made nests that were not deserted vulnerable to nest failure from other causes, e.g. predation, I compared fates of 110 unparasitized and 35 parasitized but not deserted nests, all from May. Among unparasitized nests were 19 successes (17%), among parasitized nests 5 (14%); median active life was the same. Because of this result, parasitized but not deserted nests are included in the sample analyzed next.

PREDATOR-CAUSED NEST FAILURES AND DISAPPEARANCES

Nest failures.—As just seen, 82.1% of all nest failures were caused by factors other than the cowbird. Most of these whole-brood losses I attribute to predators, although usually I simply found the nest after failure. Humans and domestic animals very rarely visited the area, and all predators were probably wild.

Analysis is of 258 nests whose failures were not cowbird-caused, all found before failure. Dates of failure are representative of all Prairie Warbler nest-failure dates during the study. Predators appeared responsible for 250 (96.9%) failures in this group. Thus predation probably caused 79.6% of the warbler's whole-brood losses ($96.9\% \times 82.1\%$, the proportion of non-cowbird failures). Lack (1954: 77) estimated that "over three-quarters of the losses of eggs and young [of open-nesting song birds] are due to predation"; see also Ricklefs' (1969: 4, 6) tabulation of nest losses in passerines.

Only two predator-caused failures appeared to have stemmed from death of an adult warbler. The nests were surrounded by feathers, the eggs intact. All other predation was on nest contents.

Proportions of predation-caused failures at various dates can be adequately inferred from information presented immediately above on dates of cowbird-caused losses, since these two causes together produced 97.5% of all the Prairie Warbler's failures.

Net effect of predation on production.—Chapter 32 estimated production of a hypothetical parasitized population whose nests were preyed upon at study-area rates. Using the same methods with a single exception to be described, I estimated production of hypothetical populations (1) parasitized by cowbirds but free from nest predators and (2) neither parasitized nor preyed upon (neither calculation shown). The one difference in method is that the calculations in Chapter 32 used 0.91 warblers and 0.91 cowbirds as the brood size of successful parasitized nests, whereas in the calculations here 0.78 warblers and 1.11 cowbirds were used. The ratio 0.91 warblers:0.91 cowbirds was produced by nests exposed to predators, which sometimes took cowbirds and not warblers (p. 388). The ratio 0.78:1.11, because it is more favorable to the cowbird and based only on nests producing cowbird fledglings, appears a better estimate for a predator-free environment.

Unparasitized, unpreyed-upon females suffered losses only from weather, defective nest construction, ectoparasites, and failure of eggs to hatch. One hundred such females would produce 624 fledglings, 4.08 more per female (or territory; see pp. 419–420) than the observed 2.16 fledglings and 4.28 more than the calculated 1.96 produced by a parasitized, preyed-upon population (Table 133). Thus observed production was about 35% of calculated potential productivity of Prairie Warblers on the breeding schedule of southern Indiana.

Production by 100 parasitized but unpreyed-upon females would be 520 fledgling warblers and 28 cowbirds. If from 5.20 is subtracted either the observed or the hypothetical production of fledglings (Table 133) by a parasitized and preyed-upon population, the differences (3.04 fledglings per territory or 3.24 per female) represent loss attributable to nest predation. Therefore observed and hypothetical parasitized and preyed-upon populations produced, respectively, 42% and 38% of the output of the hypothetical parasitized but unpreyed-upon group.

Subtraction of 5.20 from 6.24 (the potential productivity in absence of cowbirds and predators) leaves 1.04 fledglings per female as the loss (16.7%) attributable to cowbirds in a predator-free environment. This differs little from the calculated effect (13.3%) of the cowbird on the study area population (Chapter 32), but without predation the precise causes of hosts' losses would be distributed differently: In the predator-free environment, 28% instead of 47% (see p. 395) of the deficit would stem from reduced frequency of nest success; 62% instead of 53% would result from reduction of brood size in successful nests; and 10% would be attributable to the smaller clutches (because laid later) in successful nests that replaced deserted parasitized nests.

Condition of nests following predation.—Conditions of predated nests were classified according to damage, if any, to the nest and according to the state of its contents (Table 140). No stage-specific variation in condition and no variation

with date or section of the study area were revealed; the table therefore pools data with respect to these matters. Sometimes eggs continued to disappear piecemeal after a nest had been abandoned; if all disappeared on the day of failure I classed the condition "as all contents missing."

Note that no nest was deserted with live nestlings in it (but see p. 387). The cases in which nestlings were taken but eggs left untouched are evidence of the tendency (p. 388) of some predators to prefer nestlings to eggs.

Time of day of predation.—Two failures were known to have been at night, 17 during daylight. The few failures that could be bracketed between inspections 2–3 hours apart were distributed randomly throughout the day.

Snakes as predators.—Species: The most frequently encountered snakes, Racers and Rat Snakes, are entirely or largely diurnal (see Klimstra 1959; Fitch 1963a: 394–408, 1963b). Another probable predator on warbler nests, the Milk Snake, is partly nocturnal (Minton 1972: 290; see also Shelley 1938, Mahan 1956). Also present were Rough Green Snakes, which may occasionally have eaten warbler eggs (see below), and Copperheads and Eastern Hognosed Snakes, whose terrestrial habits and (in the latter) specialized diet make them unimportant as predators on warbler nests. No snake was seen preying on a Prairie Warbler nest; but the following evidence, all involving low (1–3 m) passerine nests on warbler territories, indicate to me that Prairie Warblers did suffer. In all cases to be mentioned the nests themselves were undamaged; all contents were eaten except when observers interfered.

Glenn W. Kinser (1973), Charles F. Thompson, Michael Carey, and I observed 7 cases of predation by Racers, on both eggs and nestlings (5 Cardinals, 1 Indigo Bunting, 1 Field Sparrow). I also saw a Racer coiled around a Prairie Warbler nest that the female had deserted that day with a full clutch of eggs; the eggs were gone. Another was coiled around a deserted Yellow-breasted Chat nest. A Racer we dissected to verify the presence of Cardinal eggs also contained a nestling cowbird banded some distance away. Of special interest was the observed predation on the Field Sparrow nest: I approached the nest at 1530; a Racer 1 m long glided from the nest, which earlier had contained 4 eggs and now contained 2 nestlings and 1 pipped egg. I withdrew 15 m and watched. In about 5 min the Racer was back at the nest, and I walked forward quickly; all the nest's contents had been eaten by the time I reached it.

Rat Snakes ate one brood of Indigo Buntings (seen by me), one of Yellow-breasted Chats (seen by Thompson), and two of Cardinals (seen by Kinser and Carey); see also Nolan (1959a). I once saw a Rat Snake climb to a disused American Goldfinch nest and insert its head. A female Prairie Warbler apparently directed her distraction display at a Rat Snake near her nest; two nestlings were gone and the two remaining in it were dead.

I saw Milk Snakes eat eggs from one nest each of the Cardinal, Field Sparrow, and Yellow-breasted Chat. One of these same snakes when dissected also contained nestling Cardinals or Rufous-sided Towhees.

A Rough Green Snake, its body showing an egg-size bulge, was coiled around a warbler nest from which one egg was missing; the nest had just been or was immediately thereafter deserted. William J. Hamilton, Jr. wrote me: "While I have not recovered nestling birds from the stomachs of the Rough Green Snake,

Opheodrys aestivus, it seems likely to assume that they do eat the eggs and young of small birds." Sherman A. Minton, Jr. (pers. comm.) was doubtful that this snake would prey on contents of nests and knew of no evidence.

Dates of snake sightings: I recorded every snake seen on the study area (1961–1967) to learn whether frequency of sightings varied with date. In each year field work was about evenly distributed from April through August. Pooled sightings of the Racer, Rat Snake, and Milk Snake (only six Milk Snakes) were as follows, by half-month: 16–30 April, 27 sightings; 1–15 May, 18; 16–31 May, 15; 1–15 June, 17; 16–30 June, 16; 1–15 July, 0; 16–31 July, 2; 1–15 August, 1; 16–31 August, 1. Klimstra (1958) in Iowa and Conant (1938) in Ohio also report midsummer declines. Most Iowa sightings were of Racers and Rat Snakes (ratio about 2:1, approximately the same as mine); Racers and a congener of the Rat Snake were prominent in the Ohio data. See also Fitch (1963b).

Changes in the vegetation (and therefore the conspicuousness of snakes) probably do not account for the data. Klimstra's (1958) and Fitch's (1963b) methods were calculated to minimize this possibility, and vegetation on my study area did not change markedly and suddenly between late June and early July, as sighting frequencies changed.

Racers and Rat Snakes probably do not switch from day to night foraging in July and August. Since all but six sightings were of these species, the decline in observations evidently cannot be explained by such a switch. The Racer is diurnal (Fitch 1963a: 355, 394–395) and relies on vision in hunting (see also Klimstra 1959), and the Rat Snake is "largely diurnal" (Smith 1950: 238). Sherman A. Minton, Jr., (pers. comm.) states that on night field trips in Indiana he has never found a rat snake prowling.

Herpetologists do not refer to any habitat shift, i.e. out of shrubby fields, in midsummer (see Fitch's work on home range of marked Racers, 1963a: 385–394, and Rat Snakes, 1963b).

Although snakes could have switched diet from birds to other animals in midsummer, that alone probably would not have affected frequency of sightings. Further, Klimstra (1959) and especially Fitch (1963a: 406, 1963b) have shown that relative importance of items in diets of Racers and Rat Snakes is a function of availability. Many passerines were still nesting on warbler territories in July; availability of eggs and nestlings was high.

Snakes may be more conspicuous when seeking mates after emerging from hibernation (Klimstra 1958), and females may become less active at reproduction, which is in the middle of the summer (see dates in Fitch 1963a: 418; 1963b). This may account in part for the decline in sightings. More important, both sexes become less active in midsummer (Fitch 1963b), and some evidence indicates this is accompanied by decreased food intake. Klimstra (1959) found no Racers with empty digestive tracts among 30 caught in June, whereas 3 out of 17 had empty tracts in July and 6 out of 14 in August; he suggests these data are explained by inactivity during the hot months. Elsewhere (1958: 235) he states that climatic conditions, especially temperature, "affect more importantly [than other factors] the occurrence . . . of snakes at any given time of year" and relates this statement to "the low mid-summer snake population."

In sum, decline in snake activity probably accounted at least in part for the July rise in reproductive success of Prairie Warblers and other birds on the area. Note too that most failed nests were intact (Table 140), which was the condition of all nests we saw snakes prey upon. Finally, it seems suggestive that all but two (see pp. 415, 416) acts of nest predation that we witnessed on warbler territories were by snakes (compare Fitch 1963b). Thus the change in success from 13% in May (Table 135) to 36% in July suggests that snakes were a major limitation on warbler reproduction.

Chipmunks as predators.—Eastern Chipmunks were common and probably were an important nest predator (see the many titles on chipmunk predation in Walker *et al.* 1964: 169–170). Three times I found chipmunks about 1 m from warbler nests, all of which soon failed. As reported (p. 388), a chipmunk ate a nestling Field Sparrow and ignored three eggs in an experiment, leaving the nest in the condition (only eggs remaining) in which eight warbler nests were left by predators on the study area. A chipmunk entered one cell of a trap in another cell of which I had placed a fledgling warbler, and several times chipmunks killed passerines caught in my traps (compare Smiley 1942) and mist nets. Chipmunks also eat eggs. On the study area Kinser (1973: 187) saw one (presumably) remove an egg a day from a Cardinal nest for 3 days, twice leaving shells near the nest and once on it. Charles F. Thompson (pers. comm.) has observed egg predation, and I saw a chipmunk eat a broken Wood Thrush egg on the ground (Nolan 1974; see also Errington 1938). Within-brood losses from warbler nests and the many cases (Table 140) of desertion of nests after fewer than all eggs were taken suggest chipmunk predation (see Henderson 1932, Hostetter 1939; compare Hann 1937: 199). Note also the nests from which eggs continued to disappear after failure (p. 413).

Lawrence (1953a: 71) speaks of a Red-eyed Vireo's nest "with the bottom torn out presumably by a chipmunk," but the chipmunks that Hostetter, Henderson, Kinser, Thompson, and I saw prey on nests left them intact. They pick up food neatly with the forepaws, and their predation probably would damage a nest only if nestlings in it grasped the lining and pulled it with them when dragged out.

Other mammalian predators.—The following mammals that sometimes prey on birds' nests were present but probably not important to the warbler (because uncommon or because birds are not often eaten): Flying Squirrels (seen by me preying on a Robin's nest at night; see Stoddard 1920); Fox Squirrels (Anthony 1928: 252, Allen 1938: 417–420, Hoffmeister and Mohr 1957: 147, and Perrins 1965: 616–617); *Peromyscus* spp. (Hamilton 1941).

Damage to nests (as opposed to contents) was not likely to have been caused by snakes, rodents, or birds. The following common large mammals, which eat birds, may have been responsible: Opossum (Wiseman and Hendrickson 1950, Hamilton 1951; but see Reynolds 1945); Raccoon (Giles 1939, Hamilton 1951, Tester 1953; but see Schoonover and Marshall 1951); Striped Skunk (Dixon 1925, Stebler 1938; but see Hamilton 1936); Red Fox (Hamilton 1935, Errington 1935, Nelson and Handley 1938, Dodds 1955; but see p. 226). Dogs, though uncommon, may occasionally have overturned a low warbler nest (see Mills 1905).

Birds as predators.—Blue Jays were present and probably were significant nest predators. Thompson, inspecting the nest of a Yellow-breasted Chat, found an egg missing; next day he saw a jay remove another egg intact and leave one egg, which was gone the following day. Near the study area I saw two jays take the only nestling of Eastern Wood Pewees, leaving the nest apparently undamaged. A jay flew to a nearly completed Prairie Warbler nest and inserted its head while the female called in alarm; she abandoned immediately (see p. 142). I have found little discussion of conditions in which jays leave nests they have robbed. Thompson's and my observations indicate their predation usually would leave no traces; reports by Mayfield (1960: 182–183) and Bendire (1895: 356–357) are, respectively, consistent and inconsistent with our experiences.

Common Crows bred at the study area's edges but rarely visited the low shrubby vegetation in which most warbler nests were placed. Once a crow flew over carrying a struggling bird about the size of a well grown Cardinal nestling.

Sharp-shinned, Cooper's, Red-tailed, Broad-winged Hawks, and American Kestrels hunted over the area during the breeding season. I saw hawks kill two adult passerines (described on p. 473) but no evidence of nest predation. However, Bent (1937: 103, 245) and Forbush (1927: 107, 140) refer to nest predation by some of these species, and they may have caused a few failures.

We caught Screech Owls (see Bent 1938: 251; compare Allen 1924) in our mist nets, and Great Horned Owls (see Forbush 1927: 227, Bent 1938: 306) and Barred Owls were common in the adjoining woods and occasionally flew over the area. Owl predation probably would leave nests in damaged condition (see Hann 1937: 198–199).

WEATHER-CAUSED NEST FAILURES

Six failures, 2.5% of those not caused by cowbirds and 1.9% of all failures, apparently resulted from violent wind and rain; all eggs were on the ground. Two of the nests, in forks of slender branches, probably had been whipped about by wind; three were dislodged or were tilted; one had been on a dead vine-covered branch, which broke off. Two of these nests had not been securely anchored and had tilted with use, so that structural defects contributed to their failure.

ARTHROPOD-CAUSED NESTLING LOSSES

Failures caused by blowflies.—Blowflies appeared to be a small but not negligible factor in the warbler's reproductive success, their importance probably minimized by overriding losses caused by predators and cowbirds (compare conflicting opinions about other bird species; see Stoner 1936: 216–219, Mason 1936, Neff 1945, Hall 1948: 183, Lack 1954: 78). The following paragraphs update earlier papers (Nolan 1955, 1959b) reporting collection of maggots (*Protocalliphora metallica*, syn. *Apaulina metallica*; also *Protocalliphora* new sp.: Calliphoridae) in Prairie Warbler nests. Most determinations of calliphorids are my own, based on gross resemblance to maggots determined by C. W. Sabrosky. (I allowed some maggots to pupate and examined imagoes.)

Two nests (0.8% of failures except those caused by cowbirds, 0.6% of all failures) failed because all nestlings died; within-brood losses also occurred. In

every instance the nests contained numerous maggots: (1) Three nestlings were underdeveloped and too small to be banded at the usual age (day 6 of life). Next day the nest held only one dead and one live bird whose skin was abnormally yellowish; the latter was dead on the following day. (2) This case was similar, except that the two emaciated dead nestlings were under the nest on day 9 of the nestling interval. From the mouth of one projected a caterpillar. (3-4) Single nestlings, both of which had shown retarded development and weakness several days earlier, died on day 7 of life in two successful nests.

Frequency of calliphorid parasitism, which was found in 17 (39%) of 44 successful nests examined, appeared to vary with date (see Neff 1945). Per half-month (egg 1 date), maggots occurred as follows: 1-15 May, in none of 3 nests examined; 16-31 May, in 2 of 8 nests; 1-15 June, in 8 of 13 nests; 16-30 June, in 4 of 9 nests; July, in 3 of 11 nests. Variation according to nest height, height of nest plant, or year was not suggested.

Failures caused by other arthropods.—Russell Mumford and I collected mites and Mallophaga from Prairie Warblers and their nests (see Chapter 38). Irritation from bites of these and other arthropods might occasionally cause older nestlings to leave the nest prematurely and die (compare Neff 1945). Two nestlings 6 days old were found below nests when neither weather nor spilling seemed responsible; and three 5-day-old nestlings, much chilled, lay below a nest in which were many ants, *Tapinoma sessile* (Say) (determined by M. R. Smith). I put these young back in the nest; they left when 2 were 8 days old and one was 7 (compare Chapter 27); ants were still present and may have been responsible.

PRODUCTION OF NESTS, EGGS, AND FLEDGLINGS PER FEMALE DURING FULL SEASON

Reproduction of females observed for full season.—Individuals under daily observation throughout a full season numbered 70, including a few unbanded females whose identities were established by continuity in behavior. In considering the data from these 70 birds, note that they are not a representative sample of the female population (see Chapters 30 and 31).

I counted only nests that were completed, including four in which no egg was laid (see p. 185). Counts of eggs laid and hatched were made as described on page 397 and are approximate for reasons given there. Number of fledglings produced, i.e. young that left the nest at a normal age for leaving, excludes cowbirds. Despite the discussion on page 401, no location-specific differences between the University Farm and Griffey appeared in the data, and results are pooled.

Extreme numbers of nests built per female were 1 and 7. The mean was 3.2 (Table 143), the mode 3. Number of nests built depended very largely on degree of success in escaping nest predation: some females (7%) raised fledglings from their first nest and attempted no second brood. The female that built 7 nests never succeeded; she began to build on 11 May, and her last nest failed on 13 July. Similarly, a female that on 7 July laid the final egg in her fifth nest was able to incubate all day long that day for the first time in the season; her earlier nests had failed during laying (she also had built four fragments; see Chapter 12).

TABLE 143
REPRODUCTIVE EFFORT AND PRODUCTION OF FLEDGLINGS BY 70 FEMALES
OBSERVED FOR A FULL SEASON¹

Nests ² built (N = 222)			Eggs laid ⁴ (N = 764)		
Nests/season	Females		Eggs/season	Females	
	N	% ³		N	%
1	5	7	1-4	4	6
2	16	23	5-8	18	26
3	23	33	9-12	26	37
4	17	24	13-16	16	23
5	7	10	17-20	5	7
6	1	1	21	1	1
7	1	1			
Total	70	100	Total	70	100
Mean	3.2 (SD 1.2)		Mean	11.0 (SD 4.0)	
Median	3.1		Median	10.4	

Eggs hatched ⁴ (N = 300)			Fledglings ⁵ (N = 173)		
Eggs/season	Females		Fledglings/season	Females	
	N	% ³		N	%
0	3	4	0	21	30
1	1	1	1	0	0
2	0	0	2	9	13
3	17	24	3	16	23
4	29	41	4	18	26
5	3	4	5	2	3
6	5	7	6	3	4
7	8	11	7	1	1
8	4	6			
Total	70	100	Total	70	100
Mean	4.3 (SD 1.9)		Mean	2.5 (SD 1.9)	
Median	4.0		Median	2.8	

¹ Females present from the beginning of the season until at least 25 June form the sample. A female was counted once for each year in which she provided data.

² Nests include only completed structures; no eggs were laid in four nests.

³ Percentages as rounded do not total 100.

⁴ Some nests were too high to permit inspection of the contents, and numbers of eggs laid and hatched are approximate; see page 397 for the methods.

⁵ A fledgling is a young Prairie Warbler that left the nest at the end of a normal nestling interval (see Chapter 28).

Extreme numbers of eggs per female were 4 and 21; the mean was 11.0, the mode 9-12, inclusive. (In an experiment described on p. 171, a female laid 27 eggs in 9 nests.) Mean number of eggs hatched per female numbered 4.3, about 39% of the mean number laid. About 4% of all females had no eggs hatch.

Mean production of fledglings was 2.49 per female. Twenty-one of the 70 birds (30%) produced none; 34 (49%) produced 3 or 4; the most successful female brought off 7. Five females (7%) raised 2 broods.

Reproduction of a representative sample of females.—Methods: In reproductive effort and success, females that did not change mates during the season differed from females that did change. The latter devoted less time to breeding, partly because they inevitably lost time in moving and finding new mates (and not all paired again; see pp. 352, 354) and partly because they quit breeding earlier (see p. 425). Early termination of breeding deprived them of the higher success

TABLE 144
REPRODUCTIVE EFFORT AND PRODUCTION OF FLEDGLINGS ON 129 TERRITORIES
OBSERVED FOR A FULL SEASON¹

Reproductive effort	N	Extremes	Production per territory	
			Mean	SD
Nests built	400	1-9	3.1	1.4
Eggs laid ²	1393	3-29	10.8	4.8
Eggs hatched ²	521	0-11	4.2	2.7
Fledglings ³ produced	278	0-8	2.2	2.2

¹ Territories were inspected daily until at least mid-July.

² See sample 2 methods, page 397.

³ A fledgling is a young Prairie Warbler that left the nest at the end of a normal nestling interval (see Chapter 28).

rates of late June and July. Thus a sample of females that is representative of the population must include both individuals that did not and those that did change mates. To obtain such a sample this section uses the method described on pages 348-349, and for the same reason as stated there. Data were taken from 129 territories that I inspected approximately daily (1956-1965), finding probably every nest built and certainly every one that succeeded. The critical question, whether mean production per territory is the equivalent of mean production per breeding female (and male, since the sex ratio was balanced; see Chapter 31), is considered below and the conclusion reached that the two are probably interchangeable.

A territory's production varied according to the sexual bond(s) formed on it (Table 117 and text). The sample to be analyzed includes the 104 territories whose bonds and productivity were presented in Table 117 as well as 25 others about whose bonds I lacked some fact (e.g. whether a male's relationships with two females overlapped in time). All evidence suggested that data from these 25 were congruous with those from the 104 whose bonds I know, and they were added to increase scale.

Methods of counting nests, eggs, and fledglings are described for sample 2 (p. 397).

Results: Table 144 presents numbers of nests built, eggs laid and hatched, and fledglings produced; see Table 133 for other data. On 53 territories (41%) no fledglings were produced (see Table 133). All means per territory are smaller than means per individual female studied for a full season (Table 143), but only number of fledglings per territory is notably smaller (2.16 as compared to 2.49). Even this difference (13%) is nonsignificant (Mann-Whitney U test), because of the great variability in the territory data.

Discussion: It is necessary to consider whether effort and production per territory per season is equivalent to production per breeding female (and male).

For these two to be accepted as equivalent it must appear that reproductive conditions on the study area were typical of conditions in the region surrounding it. If females that bred both on the study area and off it in a single season encountered the same conditions wherever they bred, then reproductive activities and success while off the area can be inferred from data provided by females breeding on the area. Stated otherwise, the partial histories of two individuals

TABLE 145
REPRODUCTIVE EFFORT AND PRODUCTION OF FLEDGLINGS BY FEMALES
OBSERVED FOR A FULL SEASON,¹ ACCORDING TO AGE OF FEMALE²

Reproductive effort	Age of female							
	Older than 1 year (N = 32)				1 year (N = 11)			
	Median	Mean	SD	Extremes	Median	Mean	SD	Extremes
Nests built	3.4	3.3	1.3	1-7	3.0	3.1	0.9	2-5
Eggs laid ³	10.8	11.4	4.5	4-21	10.0	9.7	2.2	6-14
Eggs hatched ³	4.1	4.1	1.4	0-7	3.3	3.7	2.1	0-8
Fledglings ⁴ produced	3.1	2.7	1.9	0-6	2.7	2.5	2.1	0-7

¹ Only females present from the beginning of the season until at least 25 June are included.

² A female was counted once for each year in which she provided data.

³ For nests too high to be inspected, numbers are approximate. See page 397 for methods.

⁴ A fledgling is a young Prairie Warbler that left the nest at the end of a normal nestling interval (see Chapter 28).

observed, respectively, in the first and second halves of the season would be the statistical counterpart of a full history of one individual. Grounds for believing that productivity and other population dynamics of the study area were representative of those in a larger surrounding region are described on pages 348 and 468-469.

Even if the study area was representative, it is also necessary that total reproductive effort and production on the 129 territories be divided by an appropriate number, i.e. one producing means equal to mean production per female. The problem is that breeding was not continuous on the 129 territories. But although for parts of the season some territories were occupied by no female and sometimes by no male, I believe that 129 is the correct divisor. That breeding was not everywhere continuous is the expected result of (1) the existence of polygyny in a population with a balanced adult sex ratio and (2) loss of breeding time because of frequent dissolution of sex bonds.

In sum, the effort and production per territory shown in Table 144 is probably a good estimate of the effort and production per male and female. Compare Thompson and Nolan (1973: 162-164); compare also the results produced by the foregoing territory analysis with estimates of production by other parulids (Hann 1937: 198, Mayfield 1960: 204, Roberts 1971).

Variation according to age of female.—Old females probably produced more fledglings than did yearlings. Old females observed for a season numbered 32, yearlings 11; ages of other females observed a full season were unknown. Means and medians of all measures of reproductive effort and productivity were higher for old females (Table 145), but only numbers of eggs laid (Mann-Whitney U test: $z = 2.52$; P two-tailed = 0.01) and hatched (Mann-Whitney U test: $z = 2.40$; P two-tailed = 0.02) were significantly greater than the relevant numbers for yearlings. Only one of the 11 yearlings (9%) laid more than 11 eggs, viz. 14 eggs; but 14 of the 32 old females (44%) laid more than 11 eggs and 11 of these 14 laid 15-21 eggs (see generally Lack 1966).

Variation according to age of male.—Old males were more productive than yearlings. The mean number of fledglings produced per territory of 40 old males at Griffey was 2.4, the median 2.0; for territories of 16 yearlings or probable yearlings

TABLE 146
ANNUAL REPRODUCTIVE EFFORT AND PRODUCTION, TERRITORIES¹ OBSERVED
FOR A FULL SEASON

Year	Cases	Nests built		Eggs laid ²		Eggs hatched ²		Fledglings ³ produced	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
1952	13	2.9	1.4	11.8	4.5	6.0	3.1	3.0	2.4
1953	14	2.6	1.3	9.6	4.9	5.2	2.4	2.1	2.5
1954	14	2.9	1.2	10.8	4.1	3.9	3.0	2.2	2.8
1957	15	3.3	1.7	11.1	5.3	4.1	2.3	2.1	2.4
1958	15	3.3	1.2	11.3	4.4	3.6	2.6	1.9	1.8
1959	11	3.2	1.3	11.7	5.2	4.5	2.5	3.3	1.4
1960	13	3.0	1.1	8.7	2.5	3.3	1.9	2.1	2.1
1961	14	3.7	2.0	12.4	6.3	3.6	3.2	1.8	1.6
1962	11	3.3	1.0	11.0	2.9	3.0	2.0	1.4	2.5

¹ Only territories inspected daily until mid-July or later and only years in which at least 11 territories were studied are included.

² See sample 2 methods, page 397.

³ A fledgling is a young Prairie Warbler that left the nest at the end of a normal nestling interval (see Chapter 28).

(see p. 22) the mean was 1.9, the median 1.5. In a Mann-Whitney U test $z = 2.40$; P two-tailed = 0.02. Note that old males had larger territories than yearlings, and territory size was positively correlated with form of sexual bond and productiveness (Chapter 29; compare Ralph and Pearson 1971).

Annual differences.—Table 146 presents statistics for 9 years in which I knew the extent and result of the reproductive effort on 11–15 territories. (The tendency toward decreased production in the 1960's did not continue after the study ended.) Differences among measures of effort and success were not significant (Kruskal-Wallis analyses of variance). It is unlikely that effort and production were constant over the years; either variation around a mean or some more complex variation, e.g. cyclical, would be expected. Factors that could cause annual variation have been considered on page 401.

To show which measures tended to vary in parallel, annual figures for each measure were divided by the overall (long-term) means for the 129 territories (Table 147). Annual quotients, as percentages of the overall means, are graphed in Figure 36. Certain conclusions follow: (1) Nests built and eggs laid per

TABLE 147
ANNUAL MEAN REPRODUCTIVE EFFORT AND PRODUCTION PER TERRITORY
EXPRESSED AS PERCENTAGES OF OVERALL MEANS¹

Year	Nests	Eggs laid ²	Eggs hatched ²	Fledglings ³
1952	94	109	143	136
1953	84	89	124	95
1954	94	100	93	100
1957	106	103	98	95
1958	106	105	86	86
1959	103	108	107	150
1960	97	81	79	95
1961	119	115	86	82
1962	106	102	71	64

¹ Each mean shown in Table 146 was divided by the means for the 129 territories analyzed in Table 144; the quotients are expressed herein as percentages.

² See Sample 2 methods, page 397.

³ A fledgling is a young Prairie Warbler that left the nest at the end of a normal nestling interval.

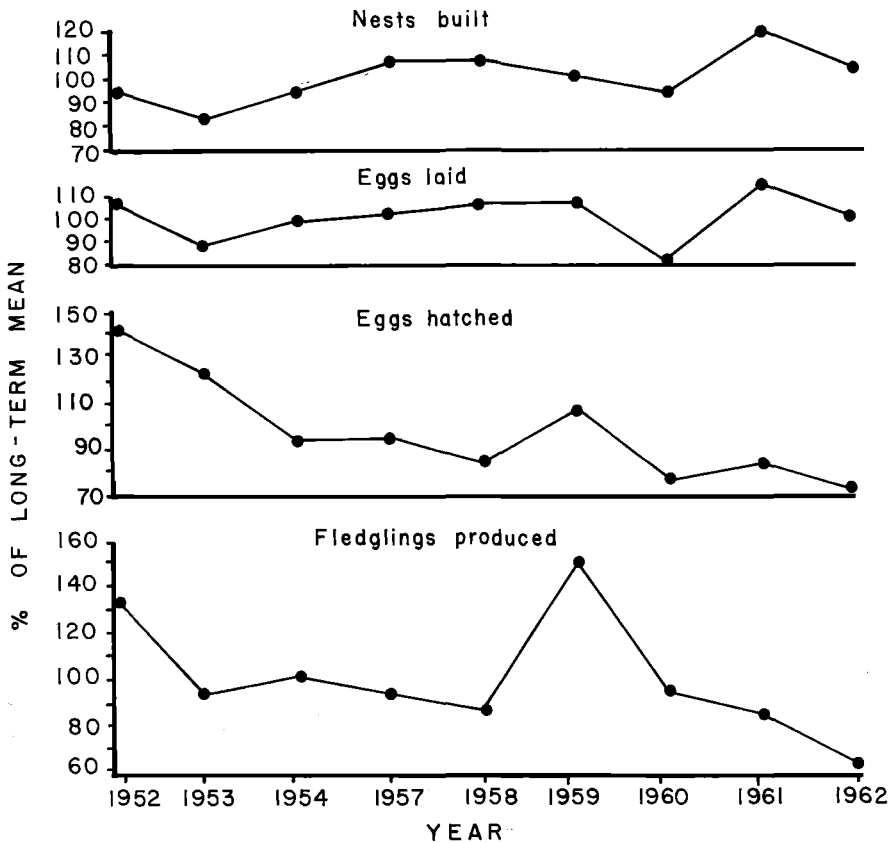


FIGURE 36. Numbers of nests built, eggs laid, eggs hatched, and fledglings produced in 9 years, expressed as percentages of long-term annual means. See Table 147.

territory varied little from year to year, and their fluctuations appear to have been positively correlated. Annual differences in date of end of breeding (therefore in clutch size; Chapter 18) and in frequency of nest failure during laying could modify the relationship between numbers of nests built and eggs laid. (2) Eggs hatched and, especially, fledglings produced fluctuated considerably, also frequently varying in parallel. (3) Slight differences in proportion of nest successes probably result in a misleading indication of great (64%–150%) annual fluctuation in fledgling production. Positive correlation would be expected between numbers of nests built (and eggs laid) and fledglings produced but only in very large samples. There is no similarity between the curves for nests built and fledglings produced, and the correlation is actually nonsignificantly negative. The explanation probably lies largely in annual differences in date of end of nesting and seasonal differences in rate of success. A slight reduction in number of late nests considerably depresses fledgling production but not number of nests per territory; and in years of late nesting small increases in number of late nests elevates fledgling production out of proportion to increase in nests per territory.

CHAPTER 34

THE TIMING OF THE END OF BREEDING

FIRST BROODS

Dates of latest nests of individual females.—Dates at which individuals began the final nest in an effort to raise a first brood on the study area ranged between 25 April and 17 July (Table 148); the mean of 186 cases was 11.2 June (SD 18.5 days). A female is counted once for each year she was present.

A female's last effort on the study area was not necessarily her last nest of the season; many left in midseason and doubtless renested elsewhere (see Chapters 29, 30, and 31). Therefore one source of variation in Table 148 was differences in fidelity to the first mate or his territory, the most faithful females contributing generally later nesting dates. A second and probably greater source of variation was heavy nest predation (see Chapter 33) and repeated renesting by females that did not leave the area. Table 149 shows percentages of nests replaced, according to date of failure. To summarize the table, prior to 15 May females almost invariably (44 of 45 cases) remained and renested. Replacement continued at a rate of about 89% in the period 16 May–15 June and 74% in the last half of June, then declined very rapidly. After 10 July, only two females replaced first-brood nests.

Dates at which females quit breeding.—Rough estimates, below, of proportions of females still capable of breeding at various dates are based on dates and/or rates of (1) nest replacement (Table 149), (2) second-brood nesting (Table 156, below), (3) midseason pair formation (Chapter 11), and (4) onset of molt, which was closely associated with termination of breeding after nest failure (Chapter 41). Estimates are rough because of the uncertainty as to whether disappearing females subsequently nested off the study area; further, even females known not to have renested may have passed out of breeding condition well before the final nest of the season failed. In comparing the estimates that follow with percentages in Table 149, it should be remembered that the proportion of females no longer in breeding condition was cumulative. For example, Table 149 can be interpreted to mean that 48% of females whose nests failed 1–5 July were unable to replace them; that group must be added to the females that had passed out of condition earlier.

Estimated proportions of the female population in breeding condition at various dates follow: 15 June—90–100%, 25 June—50–60%, 5 July—15–25%, 15 July—1–2%, 20 July—0%.

Variation in end of breeding, according to age of female.—Young females probably quit breeding earlier than old. Analysis is based first on a comparison of renestings and failures to renest between 16 June and 5 July, inclusive. This period was selected because in it some females still could breed while others could not, thus providing the necessary variation. Table 150 shows that 73% of females older than

TABLE 148
DATES ON WHICH 186 FEMALES¹ BEGAN FINAL FIRST-BROOD NESTS²
ON STUDY AREA

Date	N	Date	N	Date	N
25 April	1	21-31 May	26	21-30 June	48
1-10 May	10	1-10 June	26	1-10 July	21
11-20 May	18	11-20 June	32	11-17 July	4

¹ A female is counted once for each year she was present.

² A completed nest is counted whether or not eggs were laid, provided the female laid in at least one nest on the study area during the year.

1 year replaced nests lost, as compared to 47% of yearlings. The difference is short of significance but, in conjunction with the evidence that follows, seems suggestive.

(1) Of 18 nests begun after 25 June by females of known age, 17 were those of old birds, although that age class constituted only 65% of the population (see Chapter 38). Similarly, only three yearlings began to lay in July (latest date 3 July), whereas in the female population as a whole July first-egg dates (latest 23 July) were not uncommon (e.g. Table 46 reports 32 July nests). (2) Among females of known age, 16 yearlings deserted males between start of breeding and 30 June, as compared with only 12 older females, an age class twice as numerous. Thus at least as many yearling females as old females probably had no mate in midseason and in that sense were available to form pairs. However, no case of pair formation by a yearling fell after 20 June (Table 25 and discussion); in contrast 11 older females paired between 20 June and 10 July. (3) End of breeding and onset of postnuptial molt were closely associated in females, and yearling females molted before old birds (Chapter 41).

TABLE 149
NUMBERS AND PERCENTAGES OF FIRST-BROOD NESTS REPLACED AFTER
FAILURE, ACCORDING TO DATE OF FAILURE

Nest failures		Replacements ¹	
Date	N	N	%
1-5 May	2	2	100
6-10 May	18	18	100
11-15 May	25	24	96
16-20 May	36	34	94
21-25 May	40	37	93
26-31 May	34	28	82
1-5 June	31	29	94
6-10 June	34	29	85
11-15 June	29	25	86
16-20 June	28	20	71
21-25 June	28	22	79
26-30 June	28	20	71
1-5 July	21	11	52
6-10 July	7	2	29
11-18 July	17	2	12
19- July	9	0	0
Totals	387	303	

¹ Both for purposes of tabulating failed nests and nests that replaced them, a completed nest is counted whether or not eggs were laid in it. Data from a single female will appear in several rows if she persisted in replacing nests.

TABLE 150
FREQUENCY OF REPLACEMENT OF NESTS THAT FAILED¹ 16 JUNE–5 JULY,
ACCORDING TO AGE OF FEMALE

Age of female	Nest failures	Replacements	
		N	%
Older than 1 year	37	27	73
Yearling	17	8	47

¹ Both for purposes of tabulating failed nests and nests that replaced them, a completed nest is counted whether or not eggs were laid in it.

Variation in end of breeding, associated with date of pair formation.—Many females (14 of 29 cases) that formed pairs in midseason made only one nesting attempt on the study area and quit after that failed; even those that nested there more than once tended to quit breeding earlier than those that had been paired on the area from the beginning of the season. Table 151 shows this difference in comparing the two groups with respect to numbers that renested after failure between 16 June and 30 June; adj. Chi-square = 10.7; df = 1; $P \approx 0.001$.

Most of the females pairing in midseason had bred elsewhere as shown by their incubation patches (see Chapter 20); probably they had deserted an earlier mate (see Chapter 30). The failure of some of these birds to renest persistently on the study area may be attributable to a second desertion and a move to the territory of yet another male off the area; perhaps some females regularly formed less stable pair relationships. However, this suggestion could account for only some of the variation in Table 151: pairs formed late in the breeding season were not numerous (see Chapter 11). Therefore most females that did not renest probably had passed out of reproductive condition, doing so earlier, on the average, if they had paired in midseason. Possibly desertion of the first nest of the season and early termination of breeding after pairing with a second male had a common cause.

Annual differences in date of end of breeding.—Year-to-year differences probably existed in date of end of breeding, as suggested by annual nest-replacement rates late in the season, i.e. after failures from 16 June onward. I have weighted cases of replacement according to lateness of date, grouping them into three intervals: 16 June–25 June, 26 June–5 July, and 6 July–end of season. Nests started in these intervals are scored 1, 2, or 3, respectively; and the total score

TABLE 151
FREQUENCY OF REPLACEMENT OF NESTS THAT FAILED¹ 16 JUNE–30 JUNE,
ACCORDING TO DATE FEMALE PAIRED ON STUDY AREA

	Nest failures	Replacements	
		N	%
Pairs formed at beginning of season ²	50	38	76
Pairs formed in midseason ²	13	3	23

¹ Both for purposes of tabulating failed nests and nests that replaced them, a completed nest is counted whether or not eggs were laid in it.

² Terms are defined on page 89.

TABLE 152
ANNUAL VARIATION IN END OF BREEDING SEASON

Year	Nest failures, 16 June– 11 July	Nests replaced after failures, 16 June– 11 July	Date of start of latest nest	Lateness- of-nesting quotient ¹	Date of noticeable decline of song ²
1952	8	7	18 July	2.0	— ³
1958	12	9	7 July	1.3	17 July
1963	7	5	4 July	1.1	17 July
1961	17	11	19 July	1.0	15 July
1960	10	6	4 July	0.9	15 July
1957	14	7	5 July	0.9	— ⁴
1962	11	4	13 July	0.7	12 July
1954	9	2	30 June	0.4	5 July

¹ See pages 425–426 for method. The higher the quotient, the later the breeding season is considered to have ended.

² See page 427 for method.

³ Data were not reliably recorded.

⁴ Song declined noticeably on 8 July, revived 13 July–15 July.

for each year is divided by number of opportunities to renest (i.e. nest failures) between 16 June and 11 July that year, producing a “lateness-of-nesting quotient.” (Failures after 11 July are excluded from divisors because there were only two replacements so late; years were therefore alike in that females almost never renested that late in July.) The method assumes that distribution of nest failures among the three periods was approximately the same in the years compared, as was true. Distribution of other factors probably associated with variation (see above) was also roughly constant. Obviously the method is too crude to attach importance to minor differences in annual quotients, but large differences would suggest real variation.

Table 152 shows quotients of years in which at least seven nests failed after 15 June, arranged in descending order. Numbers of failures and replacements, dates on which the late nest was begun, and dates on which song declined noticeably are also presented. (Decline of song is discussed on page 427 in connection with annual differences in behavior of males.) When lateness-of-nesting quotients and dates of noticeable decline of song in years for which both dates are available (1954, 1958, 1960, 1961, 1962, and 1963) are separately ranked, in a Spearman's rank correlation test for association $r_s = 0.97$; $P < 0.01$ (one-tailed). It therefore seems justifiable to search for factors associated with the suggested annual variation in end of nesting.

Decline of singing and end of nesting were almost certainly not related as cause and effect; more likely both were dependent on the same or similar environmental factors. Evidence that cessation of song did not cause females to quit building nests is the fact that in all but 1 year males continued frequent singing beyond the date the latest nest was built. Nor did end of building by females induce termination of singing; the males that sang latest were usually those whose mates had left them (see Andrew 1961: 549–554).

Among environmental factors that may have affected the end of breeding, only weather can be investigated in retrospect, from official records. I considered whether June and/or early July temperatures and precipitation were correlated with the quotients in Table 152. Mean temperature in late June and July showed

TABLE 153
REPLACEMENT OF NESTS FAILING 16 JUNE–30 JUNE, ACCORDING TO NUMBER
OF PREDECESSOR NEST IN SERIES BUILT¹ BY FEMALE IN SAME SEASON

Number of nest ²	Cases of failure	Replacements	
		N	%
2	25	20	80
3	26	19	73
4–7	12	10	83

¹ In this table only nests in which at least one egg was laid are included as nests previously built.

² Nests are ranked only for females that bred on the study area from the beginning of the season.

no consistent relationship to lateness of nesting, but a relationship with precipitation is suggested if attention is focused on years with extreme quotients (Spearman's rank correlation coefficient for all years is nonsignificant). In the 2 years (1954, 1962) with the lowest quotients, rainfall between 16 June and 11 July was lighter (32.5 and 27.4 mm, respectively) than in any year but 1 of the 8 tabulated. In the 2 years (1952, 1958) with the highest quotients, rainfall between 16 June and 11 July was heavier (114.0 and 117.3 mm, respectively) than in any year but 1 of the 8. It therefore seems possible that abundant moisture was associated with prolonged breeding.

End of breeding and number of nests already attempted.—Sixty-three nests that failed between 16 June and 30 June could be ranked according to their sequence in the season's series built by individual females. The proportion of second, third, etc., nests that were replaced is shown in Table 153 (compare Table 37). Only nests in which eggs were laid are included in a female's series, and only females that were present all season are considered. Whether a female replaced a nest that had failed appears not to have been associated with the number of her previous nesting efforts (see also pp. 170–172).

End of breeding and stage at which preceding nest failed.—It is unlikely that stage of reproduction at the time a nest failed had any effect on whether the female replaced the nest or quit breeding for the year. Table 154 presents data on this point from the period prior to 16 June and also from 16 June–30 June, when any difference in replacement rate might be likely to show up. No difference appears; a Chi-square test of renesting after failure during laying, incubating, and caring for nestlings in the last half of June does not approach significance. (See also the analysis of pair dissolution as related to the stage at which nests failed, pp. 353–354.)

Noticeable decline of song.—By early July, singing was considerably reduced from its mid-June frequency, in part because more males were tending young, which caused them to sing less (see Chapter 8), and in part because some evidently had passed out of breeding condition. The approximate annual "date of noticeable decline of song" is the earliest date in July on which I heard no songs from half the males whose territories I inspected for at least 15–20 min during good weather and prior to 1230. The latest such date was 17 July and the earliest was 5 July; the mean of 11 cases was 13 July, the median 11 July. From the date of noticeable decline onward, song diminished rapidly; in all years only occasional songs were heard by 20 July.

Yearlings probably tended to quit singing before older males; no known yearling

TABLE 154
FREQUENCY OF NEST REPLACEMENT BEFORE AND AFTER 16 JUNE,¹
ACCORDING TO STAGE AT WHICH PREDECESSOR NEST FAILED

Stage at failure	Before 16 June			16–30 June			Difference in % between periods
	Failures	Replacements		Failures	Replacements		
	N	N	%	N	N	%	
Active building ^a	7	7	100	1	1	100	—
Inactive building ^a	21	19	90	1	1	100	—
Laying ^b	66	63	95	13	7	54	41
Incubation ^c	129	117	91	45	34	76	15
Nestling	24	19	79	18	12	67	12

¹ Nests that failed after 30 June are excluded.

² Phases of building are defined on page 149.

³ The laying interval began with laying of egg 1 and ended with laying of the final egg.

⁴ In this table the incubation period began with laying of the final egg and ended with hatching of the first egg to hatch.

was heard as late as the year's date of noticeable decline of song. A male banded in the nest and studied as a yearling sang last, so far as known, 3 days before the date of noticeable decline; in the next 2 years he sang much later relative to those years' dates. (Yearling males molted earlier than old males; see Chapter 41.)

Very hot weather in early July sometimes was associated with reduction of song, cooler wetter weather with its persistence. In 1957, singing declined noticeably on 8 July, the second earliest such date, but revived on 13 July immediately following 27 mm of rainfall. The 2 years of earliest noticeable decline of song (1954, 1957) were alike in producing little rainfall in the first 10 days of July and in being very hot between 6 July and 10 July, when singing waned. The 2 years with the latest decline of singing (1958, 1963) were the opposite. However, some years (1959, 1961) did not fit this pattern.

Responses of males to female desertion.—In 66 cases males lost females after 15 June, and their subsequent behavior provides some evidence of their condition. Some advertised; some left their territories (Chapter 35); and some remained but became silent, began to molt, and were rarely seen. While the first two of these responses are not decisive that such males were or were not in breeding condition, nevertheless, if the three kinds of behavior are distributed by date (Table 155), a suggestive pattern emerges.

To summarize, until 5 July, 20-25% of the deserted males disappeared or quit singing no more than 1 day after losing mates; between 6 July and 15 July, 37% did this; the proportion then increased to 78%. At the opposite extreme were males that either advertised for more than 10 days or that acquired new mates before 10 days had passed. Between 16 June and 5 July, 50% fell in this category; an additional 16% advertised 6-10 days. This suggests that until 5 July at least 66% of males were still capable of pairing and breeding. If the same assumptions about significance of song are applied to 19 males deserted 6 July-15 July, 32% of this group were still in breeding condition.

If the preceding paragraph is approximately correct, males tended to remain in reproductive condition a little longer than females. Certain episodes also suggest this: (1) A male that lost his mate on 8 July advertised loudly and steadily until I stopped visiting his territory on 24 July, far beyond the latest date of rene-

TABLE 155
BEHAVIOR OF 66 MALES FOLLOWING MATE'S FINAL DISAPPEARANCE LATE
IN BREEDING SEASON, ACCORDING TO DATE OF DISAPPEARANCE

Behavior of male	Date of female's disappearance				Totals
	15-25 June	26 June-5 July	6-15 July	16-27 July	
Disappeared	5	4	7	7	23
Advertised and remated	3	4	0	0	7
Advertised unsuccessfully					
2-5 days	2	2	6	1	11
6-10 days	2	4	5	1	12
10+ days	6	6	1	0	13
Totals	18	20	19	9	66

by a female. A neighbor's mate entered his territory 18 July-22 July to forage for nestlings and was courted as intensely as she would have been in late April. (2) Several pairs lost nests late in the season and remained together 1-2 days, the male displaying and behaving exactly as in the pre-nest-building period, the female failing to respond and then either beginning to molt or disappearing. The view that males tended to continue in breeding condition longer is inconsistent with Kendeigh's (1952: 168) generalization that the male "usually precedes the female in returning to nonbreeding condition."

Desertion of families by males.—Desertion of the family does not necessarily imply inability to breed, just as constancy in performance of parental behavior does not prove continued ability to breed. However, data on desertion late in the breeding season are suggestive, and it is convenient to present them here. On 11 closely observed territories on which nests succeeded after 1 July, males ended all attention to females and their nests before or when the fledglings left the nest. In comparison, in this same period 33 males tended young until nests were destroyed by predators or until fledglings from successful nests died or disappeared. The suggested desertion rate of 25% late in the season may be too low because those males whose nests failed did not have full opportunity to desert; some that did not desert would perhaps soon have done so had their nests remained active longer. Five of the 11 that deserted did so during the incubation period and six did so after they had begun to feed nestlings; one of the latter stopped attentive behavior when the young left the nest. Attentive behavior and singing declined noticeably just before all desertions. Some deserters disappeared, but most were seen later in the same or in another year; there is no reason to suppose that any died rather than deserted.

SECOND BROODS

Dates.—Dates (margin of error 2 days) of beginning of building of 19 initial (i.e. not replacement) second-brood nests were distributed as follows: 4 June-15 June, 5 cases; 16 June-25 June, 8; 26 June-8 July, 6; the mean was 21 June (SD 9 days). Dates on which four replacements of second-brood nests were started were 19 June, 24 June, 27 June, and 19 July. An additional nest, started on 15 July, may have been either an initial second-brood attempt or its replace-

TABLE 156
NUMBER OF PAIRS THAT ATTEMPTED SECOND BROODS,¹ ACCORDING TO DATE
FIRST BROOD LEFT NEST

Date first brood left nest	Cases	Attempted second broods	
		N	%
25-31 May	5	3	60
1-10 June	10	8	80
11-20 June	10	2	20
21-30 June	17	4	24
1-10 July	9	1	11
11-20 July	13	0	0
21-31 July	17	0	0
1-13 August	5	0	0
Totals	86	18	

¹ Only second-brood nests in which eggs were laid are included.

ment. Thus, attempts to raise second broods began about midway through the period of building first-brood nests (25 April-17 July; see Table 148), were roughly evenly distributed over the last half of that period, and ended about when first-brood attempts ended.

Relationship between date of first-brood success and second-brood attempts.—Table 156 shows numbers and percentages of females that built and laid eggs in second-brood nests, according to 10-day intervals in which first-brood young left the nest. Of females whose first young left by 10 June, 73% built and laid again on the study area; when nest-leaving was in the period 11-30 June, females made a second-brood effort on the area only 22% of the time. Only 1 female among 44 that succeeded in July nested again (on 5 July, after changing mates).

Recalling that bringing off young was the occasion for both temporary and permanent pair dissolution in several cases (pp. 121, 346, 347) and that some birds changed mates before raising second broods, it is likely that nearly all females that produced fledglings by 10 June nested again, on or off the study area. Changing mates after 10 June was not common, and the big decline of second-brood nests on the area after that day probably reflects a genuine reduction associated with advancing date. The somewhat abrupt decrease may require reconciliation with the view (p. 423) that 50-60% of all females were still able to breed on 25 June. As a conjecture, reproductive motivation of most females may have begun to wane toward mid-June; the effect of such a change may have been less on females that so far had failed to produce fledglings than on females tending first broods. The presence in mid-June of fledglings still demanding attention could have affected their mothers' behavior and diminished motivation to nest again.

Age of female and second-brood attempts.—The relationship, if any, between age and likelihood of attempting a second brood is not clear. Only 22 females that were aged brought off a first brood by 30 June. Of 18 older than 1 year, 8 (44%) built and laid in second-brood nests. Of 4 yearlings, 1 (25%) attempted a second brood. Possible differences in reproductive success of yearling and older females are discussed on page 420.

Annual differences.—At least one second-brood nest was built in all but 1 of the 11 years in which I searched for such nests; in the exceptional year no first-

brood nests succeeded early enough to make a second-brood attempt at all likely. It is suggestive that in 1954 only 1 of 6 females attempted a second brood after bringing off a first brood by 30 June (compare 4 attempts among 6 females in 1959); 1954 was also the year in which first-brood attempts ended earliest during the study (Table 152).

CHAPTER 35

THE POSTREPRODUCTIVE PERIOD

LOCATIONS AND MOVEMENTS OF ADULT MALES

The "postreproductive period" is the interval between the end of reproduction and fall migration. An individual "ended reproduction" when its last pair bond dissolved or its parental behavior terminated, whichever was later.

The sample consists of 63 color-banded males that were still on territory on 10 July and that I searched for systematically during the postreproductive period, visiting their territories at least twice weekly until 1 October. A male is counted once for each year he was studied; treatment of such cases as independent seems justifiable because some males behaved differently in different years (below).

Of the 63 males, I found 50 (79%) in the postreproductive period. Male movements at this time appeared to fall into three categories.

1. Thirty-one (49%) were seen repeatedly, never more than 200 m off the breeding territory and usually on it; apparently they were as attached to that site as they had been during reproduction.

2. Some moved considerable distances from the breeding territory, remained away for days or weeks, and then returned to it in September. Of 14 such cases (22%), 10 males left after reproduction ended in July and 4 disappeared with (i.e. while tending) family units (see Chapter 28). One or more of the 10 not caring for fledglings may possibly have been present and overlooked by me, but certainly most moved away for a time. For example, I found a male in molt 1500 m from his territory, on a site he had bred on in previous years.

3. Some (18 cases, 29%) left the breeding territory and probably did not return that year. As a test of the probability that these males were present and overlooked, I compared the number of sightings of each of the 63 males in the sample with numbers expected at random under a Poisson distribution (data not shown); $P < 0.01$. Death probably accounts for few if any disappearances. I found the postreproductive locations of five of the males. Four others returned to breed the following year; the possibility that the remaining nine died in July, which would require a high concentration of deaths at a time when no unusual hazards were apparent, is remote (see Chapter 38).

Factors possibly associated with variation.—There is no statistical evidence of association between the date the individual's breeding ended or the date his molt began or his reproductive success or failure, on the one hand, and his postreproductive movements and location, on the other. But the existence of a territory occupied at an earlier date (see Chapters 5 and 30) may have increased the probability that a male would leave his current breeding territory. Thus, of seven males that had relocated from one territory to another on the study area, four did not leave that new site in the postreproductive period; one went back to his abandoned site but returned to his new territory in September; two others

apparently spent the full postreproductive period on the former territory. In addition, a male not included in the sample because he had moved off the study area in April returned in the postreproductive period to the territory that he had abandoned in April.

Size of postreproductive home range.—Locations of males that were seen repeatedly fell within areas about as large as an average territory (Chapter 29). This was true whether the postreproductive site had or had not been the breeding territory.

Behavior of individuals in successive years.—I searched for 15 individual males in two postreproductive periods and 10 others in three periods. Of these 25, 15 probably remained on the current breeding territory in every postreproductive period in which I studied them. Ten probably left permanently in 1 or 2 years but either remained on the territory or returned to it in September in 1 or 2 other years. No male disappeared permanently in all years in which I searched for him. Using the 10 males that behaved differently in different years, I attempted without success to correlate variation in behavior with reproductive success or failure, advancing age, and territory characteristics.

LOCATIONS AND MOVEMENTS OF ADULT FEMALES

Methods were the same as for males. The sample is 54 color-banded females, almost all of them mates of the males whose behavior is analyzed above. More females than males disappeared prior to 10 July, which reduced the size of this sample.

Twenty-three (43%) of the females were found in the postreproductive period. The cases appeared to fall into three groups comparable to those for males; there was also a fourth group, in which the facts are too scanty or ambiguous to be interpreted.

1. Seven birds (13%) probably remained on or very near the breeding site; they were never found more than 100 m from it.

2. Three (6%) left the breeding site with dependent offspring and returned after these had become independent. One came back in August from 300 m away; two returned, in September and October, respectively, from unknown locations.

3. Thirty-seven females (69%) probably moved away permanently; 6 were found at their postreproductive locations. Representative cases follow: A female and her fledglings remained in an area of about 0.4 ha, 350 m from the breeding site; I saw them there 10 times in 42 days. A female remained on her breeding home range with dependent young, then in mid-August moved 600 m; I saw her at the new site 4 times in September and October. A female that brought off no young disappeared from her breeding site in July and moved 500 m to a location she occupied in the postreproductive period of 5 successive years (see p. 458).

As with males, it is unlikely that any substantial number of the 31 females that I did not find had died or were present but overlooked. An indication that females moved after breeding more often than males did is that 58% of adult males seen in the postreproductive period were banded, compared to only 41% of adult females ($P < 0.005$); this is despite a ratio of banded : unbanded breeding individuals that was lower for males than females. The high proportion of female

disappearances after breeding is consistent with the generally low site fidelity in females (see Chapters 30 and 37).

4. Seven individuals (13%) were either found on the breeding home range only once or were found on both that and another site several times in alternation.

Factors possibly associated with variation.—Reproductive success probably was not associated with fidelity to the breeding home range in the postreproductive period, but date at which reproduction ended and site fidelity evidently were associated (see Chapter 37). Of 31 females that ended breeding by 31 July, 23 were not seen again that year; of 22 that finished in August or September, 8 were not seen thereafter that year; adj. Chi-square = 6.1; $df = 1$; $P < 0.025$.

Females that were molting at the end of reproduction tended to remain on or near the breeding site. Birds whose date of end of reproduction and date of onset of molt I knew (or could estimate from observed molt states, assuming their molt had proceeded at the average rate) numbered 45. Twelve of 21 that had begun to molt when reproduction ended remained on or near the breeding home range; one of 24 that had not begun to molt when reproduction ended was seen after that date; adj. Chi-square = 12.7; $df = 1$; $P < 0.001$. Data are too few to reveal whether site fidelity was independently associated with late end of reproduction and also with being in molt when reproduction ended. However, molting birds were sluggish and sedentary (p. 435) and physiological demands probably increased during molt (King and Farner 1961: 246–248, Sturkie 1965: 256–257, Lustick 1970); therefore it seems probable that being in molt was independently conducive to remaining near the breeding home range when reproduction ended. This is even more likely if it is assumed that the energy cost of flight is higher while flight feathers are being renewed. As noted, no similar relationship between molt and remaining at the breeding site was found in males (p. 432), but bigger samples may be needed for that sex because season-long (unvarying) site attachment appeared to affect a larger proportion of individuals.

As with males, the tendency of some females to leave the current breeding location may have been reinforced by attraction to sites occupied in former years (see p. 458).

Size of postreproductive home range.—The female home range after breeding was about the size of an average territory (Chapter 29). I paced distances between 35 pairs of points at which 10 females were seen on consecutive occasions, some sightings as much as 2 weeks apart; extremes were 5 and 500 m, the mean about 100 m.

Behavior of individuals in successive years.—Because of females' low rate of return in subsequent years, little information is available on individuals' postreproductive locations in successive years. One female in a 5-year span bred on 2 different study-area sites and on at least 1 (undiscovered) location off the area, but frequent sightings indicated that she spent all postreproductive periods in a single location on the study area. Another that bred on different sites in three years was seen in the postreproductive period of each year only at her current year's breeding site. A female present during four breeding seasons was never found after her reproduction ended. A bird present in two years moved away from the breeding site (and was found by me) in both. Finally, four females did not move from the breeding site in one year but disappeared from it in another.

LOCATIONS AND MOVEMENTS OF YOUNG OF THE YEAR

"Site when last dependent" is the place at which the family unit was observed just before the end of dependence.

Soon after reaching independence young birds left the site when last dependent and apparently moved more or less randomly in the region for several weeks. In years in which intensive fieldwork continued until October, I saw 27 (11%) of 246 banded young after they attained independence. The ages of these when last seen were 40–45 days in seven cases; 46–50 days, three cases; 51–55 days, eight cases; 56–60 days, one case; 61–65 days, two cases; 66–70 days, four cases; 71–80 days, two cases. I was sure of the sex of only 8 of these birds; 4 were males, 4 females. The two oldest were a male (75 days) and a female (78 days).

Final sighting of 26 of the 27 young was on the study area; one I last saw (age 66 days) in my backyard, 3 km from its nest. Distance between final sighting and approximate center of the site when last dependent was paced or was measured on a large scale map: Extremes were 0 and 900 m, excluding the sighting in my yard; the mean of the 26 cases was 460 m (SD 373 m). In cases of young seen more than once, the final sighting was not always the one farthest from the site when last dependent.

Only one young bird, probably a male, appeared to settle down on a home range. It was seen at the same place three times between 1 September (when it was 48 days old) and 19 September. The location was 450 m from the site when last dependent. On 19 September this bird chased another young Prairie Warbler and a Tennessee Warbler there, hence may have been territorial. In contrast to the sedentary behavior of this immature, three others moved 300–450 m between sightings 6–11 days apart.

Young from early broods showed no tendency to remain near the study area longer than those from late broods, in spite of the bias caused by the fact that birds hatching early had more time available to them (before autumn) during which they could have remained. Of the 8 individuals observed on the study area at ages 61 days old or older, 5 had left the nest on or after 15 July. (Extreme dates of nest-leaving during the study were 25 May and 15 August.) The bird seen at age 78 days had hatched on 15 July and was still present on 26 September.

OTHER BEHAVIOR

Activity of adults during molt.—Birds in heavy molt flew infrequently, usually covering only a few m. They appeared reluctant to move and often did not fly even when approached noisily and closely. They also tended to perch motionlessly for 2–3 min (one male did so for 30 min at midday) and were very inconspicuous; many stayed in dense cover. I could follow and observe them without interruption for 15–20 min, which usually was impossible with Prairie Warblers not in molt. Molting birds preened, scratched, and stretched much more than at other stages of the season; some basked (perching normally, not sunbathing) in the early morning sun on cool August–September days (compare Stewart 1952, Wallace 1955: 49, Marler 1956: 148–149, Newton 1966: 61–62). No difference in the perching and foraging heights of molting and nonmolting birds was detected in either sex (median test, about 700 cases).

Vocal behavior.—Males sang least in August (Chapter 8), then increased song frequency in September-October. Estimating on the basis of proportions of songs by banded and unbanded birds, at least 75% of singers at this season were on or very near their breeding territories of the season. Songs were more common in the morning but were heard occasionally during the afternoon.

Calling and singing often seemed aggressively motivated. To illustrate, in September a male on his own territory began to call Chek, and his banded neighbor, 30 m away and also on his own territory, approached and called Harsh Cheks; simultaneously a male on a third territory joined in with Cheks. As another example, a banded male on his territory in September faced an unbanded male 5 m distant; both called Harsh Cheks; the unbanded male then flew away and the banded male sang. See also the following section.

Intraspecific fighting.—I recorded details of 30 intraspecific fights and saw many other short episodes. With few exceptions the fights were fast chases (as long as 25 m), and the attacked bird retreated almost immediately. In short chases the roles of attacker and attacked sometimes changed, apparently without reference to location (i.e. territory lines). A few males sang before or after chasing; more called Chek or Harsh Chek; many were silent.

A few encounters were intense. A male in September fought another for 5 min in the middle of one fighter's territory. This latter called Harsh Cheks throughout the fight and for several minutes thereafter; the interloper sang 8–10 group-B songs at half volume. Visible behavior was fully comparable to that in an early-season fight at a territory boundary and included parallel movement, darting back-and-forth skirmishes, supplanting, flutter-up, and gaping (Chapter 7). A male in September sang in the middle of the breeding territory of another male, which immediately approached and chased the singer. The singer instead of leaving flew in a roughly circular course around the territory, about 16 m above ground. The owner pursued closely and did not evict the singer during the 45 sec they were in sight (compare circular pursuits, Chapter 6).

In cases in which age and/or sex were known, 8 fights were between adult males, 9 between an adult male and an immature (male or unsexed), 5 between immatures (male or unsexed), one between an immature male and an adult female. Six fights were on one fighter's breeding territory; 3 were not on the territory of either; the information was lacking in the remaining cases.

Fights took place at all times of day. Those in which immature birds were aggressors were observed 1 August and thereafter, those in which adults were aggressors never before 22 August. This difference is presumably associated with the fact that most adults were molting in August; aggressiveness was never seen in a bird whose molt was not complete or nearly so.

Interspecific fights.—I noted details of 28 interspecific fights; most were chases, but a few were supplanting attacks. Occasional Harsh Cheks were the only vocalizations heard. Once an immature Prairie and a Tennessee Warbler alternated in attacking each other for 30 sec, finally coming into physical contact and pecking each other while perched. In 26 of the fights Prairie Warblers were either the apparent aggressors or they resisted aggression and sometimes took the initiative; 18 participants were adults, 8 immature.

Mixed autumn flocks of migrant parulids, many of their members mildly aggressive, appeared to cause excitement and unrest in resident Prairie Warblers (see p. 452). Species toward which the latter behaved aggressively, with numbers of cases when more than 1, were *Empidonax* spp. (2), Gray Catbird, Eastern Bluebird, Blue-gray Gnatcatcher (2), White-eyed Vireo, Blue-winged Warbler, Tennessee Warbler, Nashville Warbler, Magnolia Warbler (2), Yellow-rumped Warbler, Wilson's Warbler, undetermined warblers (2), Cardinal, American Goldfinch (4), Field Sparrow (5). An adult male once attacked an Eastern Bluebird and immediately thereafter a Cardinal, both much larger than he; bill snapping was heard in the chase of the bluebird (compare Stewart 1943).

Prairie Warblers attacked by a Blue-winged Warbler and a Brown Thrasher retreated without resistance.

Discussion of fighting.—Fighting probably was associated with gonadal activity common in many species in late summer. Its tendency to occur on one fighter's home range indicated territorial motivation; it contained no behavior peculiar to the post-reproductive period; and circumstances suggesting nonreproductive motivation, e.g. hunger, were never observed (compare Hinde 1952: especially Chapter 15). The behavior of immature birds appeared identical with that of adults and probably was the incipient reproductive fighting often seen at this season (see Hinde 1952: Chapter 13, Marler 1956: 150–151).

Gregarious behavior.—Occasionally two nonmigrating adult females or an adult female and an immature (either sex) that was not her offspring fed quietly within 2–3 m of each other for 15–20 min; such adults were not migrating, as I knew either because they were banded residents or were molting heavily (see Chapter 36). Once a molting adult male and a female foraged together for many minutes. Evidence of gregariousness in independent immature birds is described below.

(1) In about 25 cases independent young attached themselves for minutes or hours to family units; twice unbanded young were seen with such units on 2 successive days. Occasionally these birds seemed to be following the parents, at other times the fledglings (see the cases of sexual behavior, p. 320, and the possible case of helping, p. 326). In one instance I knew the ages of all involved; 2 banded 46-day-old broodmates that had recently left their father (400 m distant) joined 30-day-old fledglings and their male parent. (2) Three times two broodmates stayed together at least 1–2 days after leaving a parent and the site when last dependent. Independent young from different broods were also often seen together; this occurred until at least age 57 days. (3) Sometimes an adult male would sing and an immature not its offspring would fly to and follow it. Young Prairie Warblers also frequently associated with birds of other species, most often with mixed flocks of migrant parulids but sometimes with Carolina Chickadees and Blue-gray Gnatcatchers.

Other behavior.—Like dependent fledglings (p. 319), independent immatures often seemed attracted by man. They flew toward me in short flights, perched 3–5 m distant, and watched me steadily and quietly, usually until I moved away.

Apparent sexual behavior was seen three times after the general end of breeding, if behavior of immatures is included. (1) An immature of undetermined sex

landed 0.7 m from an immature male and cocked its tail in a position resembling female solicitation; the male did not respond, and they separated. (2) An adult male landed several cm from a small bird that I could not see clearly, raised both wings over its back, performed wing waving (p. 85), and walked about 8 cm toward the other bird. In 1 sec there was a rapid chase out of sight. (3) See page 320.

CHAPTER 36

FALL MIGRATION; EXTRALIMITAL MOVEMENTS

DATES

Among information relied on in this section are dates of fatal nocturnal collisions of Prairie Warblers with a television tower in Leon County, Florida (see Chapter 3 and Stoddard and Norris 1967: esp. 7, 24–42). Tower kills are arbitrarily treated as having died after midnight and are considered migrants because of the improbability of nocturnal movements by large numbers of local Florida residents; further, most tower-killed specimens were fat. Also relied on are dates of capture of Prairie Warblers by participants in Operation Recovery, a cooperative netting-banding project in eastern United States (see Baird *et al.* 1958, 1959). Special reliance is placed on 1963 Operation Recovery data from Island Beach, New Jersey, an Atlantic barrier beach 3–10 km off the mainland. Bertram G. Murray generously supplied many details (see also Murray 1966).

In light of what appear to be normal migration dates (below), individuals found in the breeding range in November are regarded as still-migrating stragglers, individuals seen later as no longer migrating.

Beginnings of migration.—The earliest tower kill was 15 July, the next 21 July. Sixteen individuals died in July, their deaths distributed among 5 of the 13 years during which I received all tower-killed Prairie Warblers from Stoddard. Mortality was associated with weather conditions (Stoddard and Norris 1967: 10–19) that are not usual in July, and a late-July movement into northwest Florida is probably an annual event.

The earliest known date of collection in the winter range is 20 July (Riley 1905, on New Providence, Bahamas; see also Bond 1964). At Nassau, Bahamas, Robert W. Hanlon's earliest records were 31 July and 1 August of different years (pers. comm. 1959).

The earliest Prairie Warbler captured in Operation Recovery that I am aware of (Willet J. Van Velzen and Chandler S. Robbins pers. comm.) were two individuals netted on 2 August and another 3 August along upper Chesapeake Bay, Maryland, and one netted 6 August near Ocean City, Maryland (an Atlantic barrier beach). At Island Beach, New Jersey, daily netting began on 2 August 1963, and the first Prairie Warbler was caught 15 August, after which captures were rather regular.

Table 157 presents selected published observations of earliest migration dates. Except for a vague statement by Forbush (1929: 275) that in Massachusetts some Prairie Warblers begin to move south in July and a report from Cleveland on 26 July (Williams 1950: 138), first dates are from the southern part of the range. Particularly interesting because they are both numerous and consistent are mid-August dates from Ontario, certain Lake Erie islands, and mainland Michigan; these also coincide with the 15 August date from Island Beach, New Jersey, and with observations on my study area (earliest observation of probable migrants,

TABLE 157
EARLY DATES OF FALL MIGRATION WITHIN THE BREEDING RANGE

Location	Date	Authority
Massachusetts	July	Forbush 1929: 275
Cleveland, Ohio	26 July	Williams 1950: 138
Point Pelee, Ontario	15 August	Taverner and Swales 1908: 120
Mackinac Island, Michigan	10 August	White 1893: 228
Huron Co., Michigan	10 August	Wood 1951: 405
Prince Georges Co., Maryland	31 July	Stewart and Robbins 1958: 299
Pensacola, Florida ¹	27 July	Howell 1932: 407
Gulf Coast, Mississippi	22 July	Kopman 1905

¹ Four Prairie Warblers were recorded here on 27 July 1919 and 6 on 28 July 1929. A Prairie Warbler struck the lighthouse on Sombrero Key off southern Florida on 1 August 1888.

10 August). Thus a south-to-north start of migration is indicated; this is discussed further on pages 442, 443.

Peak of migration.—Information on dates of peak migration is lacking for most of the breeding range. Peaks reported for Massachusetts are 5–15 September (Hill 1965: 261—Cape Cod), 15–22 September (Griscom and Snyder 1955: 204). Near New York City, migration becomes pronounced early in September (Cruikshank 1942: 400). In Maryland-District of Columbia the peak is 15 August–5 September (Stewart and Robbins 1958: 299). On my study area small flocks judged to be migrating were commonest in the first half of September.

TABLE 158
LATE DATES OF FALL MIGRATION¹ WITHIN THE BREEDING RANGE²

Location	Date	Authority
Maine	17 September	Palmer 1949: 481
Massachusetts	3 November ³	Hill 1965: 261
Connecticut	17 October	Sage <i>et al.</i> 1913: 159
New York City	11, 18, 29 November	Bull 1964: 386
Niagara region	22 September	Beardslee and Mitchell 1965: 385
Michigan	23, 30 September	Swales 1910; Walkinshaw 1959
New Jersey	16 October	Stone 1937: 830
Maryland	20 October, 19 November ⁴	Stewart and Robbins 1958: 299
Ohio	6 October	Borror 1950: 26
Indiana	10 October	This study
Illinois	23 November	Mumford 1960
North Carolina	15 October ⁵	Pearson <i>et al.</i> 1959: 329
Kentucky	15 October	Mengel 1965: 419
Oklahoma	1, 3 November ⁶	Sutton 1967: 511
South Carolina	23 October, 25 November ⁷	Sprunt and Chamberlain 1949: 469–470
Georgia	22, 30 October	Burleigh 1958: 540
Alabama	15, 20 October ⁸	Howell 1928: 309; Imhof 1962: 476
Florida	6, 7 November	Howell 1932: 408

¹ November records are arbitrarily assumed to be of migrating stragglers, later records to be of birds no longer migrating.

² Florida lies largely outside the range of *D. d. discolor*. Dates given are for that race.

³ A specimen was collected 2 January and another was seen next day (McKechnie 1909). Baird and Emery (1957) report a sight record from New England in December 1956.

⁴ Scott and Cutler (1966) report a sight record on 28 December. Compare the sight record from West Virginia on 2 January (Handley 1960).

⁵ Pearson *et al.* (1939: 329) report 3 December records. There are also records from nearby Cape Charles, Virginia, on 27 December (Scott and Cutler 1971) and 29 December (Scott and Cutler 1969).

⁶ Sutton (1967: 511) reports a sight record on 26 December.

⁷ Sprunt and Chamberlain (1949: 469–470) report a sight record on 9 January, and three records from late February–early March. They regard the Prairie Warbler as a permanent resident of the coast of South Carolina but rare in winter.

⁸ Imhof (1962: 476) reports sight records on 10 February and 3 March. Compare the sight record from Louisiana on 1 January (Lowery 1960: 444).

TABLE 159
NOCTURNAL MIGRANT PRAIRIE WARBLERS DYING IN COLLISIONS WITH A
FLORIDA TELEVISION TOWER,¹ ACCORDING TO DATE, SEX, AND AGE

Date	Adult		Immature		Totals
	Male	Female	Male	Female	
11-20 July	0	0	0	1	1
21-31 July	0	0	2	13	15
1-10 August	0	1	1	4	6
11-20 August	36	32	7	14	89
21-31 August	17	17	4	5	43
1-10 September	12	12	7	4	35
11-20 September	34	35	7	16	92
21-30 September	34	17	1	10	62
1-10 October	21	12	4	9	46
11-20 October	2	6	1	1	10
21-31 October	3	0	1	0	4
Totals	159	132	35	77	403

¹ See pages 21 and 439 for further details; see also Nolan and Mumford (1965) and Taylor and Anderson (1973).

Latest dates.—Table 158 presents dates of latest observations from a number of states. These suggest that most individuals leave the northern part of the breeding range (arbitrarily, north of 40°N) by the end of September and that in the south few birds are seen after mid-October.

FACTORS ASSOCIATED WITH VARIATION IN DATE OF MIGRATION

Age.—Earliest migrants: Three samples indicate that the earliest migrants are largely or entirely young of the year: (1) Mumford and I examined 403 tower kills from the period 15 July–29 October (107 days); of these, 291 (72%) were adults (skulls completely ossified). In the 26 days prior to the death of the first adult, on 10 August, 21 immature birds died or 19% of all immatures (see Table 159). (2) On Island Beach (Table 160) an immature female was caught on 15 August 1963 and six immature males between 19 August and 28 August; only one adult was caught that month, on 31 August. (3) Riley's (1905) specimen collected on 20 July in the Bahamas was immature. Among 254 adult and 256 immature museum specimens that were taken in the winter range

TABLE 160
AUTUMN MIGRANT PRAIRIE WARBLERS CAUGHT AT ISLAND BEACH,
NEW JERSEY, ACCORDING TO DATE, AGE, AND SEX¹

Date	Adult		Immature			Totals
	Male	Female	Male	Female	Unsexed	
11-20 August	0	0	0	1 ²	0	1
21-31 August	0	1	6	0	0	7
1-10 September	2	1	9	10	2	24
11-20 September	2	1	8	8	0	19
21-30 September	4 ³	2	3	3	0	12
Totals	8	5	26	22	2	63

¹ The data were supplied by Bertram G. Murray, Jr. See Murray (1966).

² The first capture was on 15 August.

³ The last captures were on 30 September.

and that I examined, 22 individuals were killed in August. Of these, 20 were immature and 2 were adult ($P < 0.001$); the latter died at the end of the month (29, 30 August). See also the following subsection.

Relation between age of earliest migrants and geographical variation in date of start of migration: The probability that onset of migration becomes progressively later from south to north (see page 440) is strengthened by the facts that the earliest migrants are young and that fledglings leave the nest earlier in the south (because nesting is earlier there; see p. 188). The first immatures produced in the south would be ready to migrate before the first produced in the north, unless rate of development and age at migration vary according to latitude; evidence on this last point is lacking.

A specific instance indicating that immatures begin moving earliest in the south is the case of the July tower-killed young birds from Florida. The following facts, when considered together, make it highly unlikely that these individuals could have been produced as far north as my study area (about 39° N): (1) Nine of the 16 July tower kills were still molting on one or more tracts (capital, spinal, ventral, and crural). Estimating conservatively from the molt condition of birds of known age on my study area, postjuvenile molt probably is complete by age 60–70 days (Chapter 28, esp. pp. 312–313); this, then, is about the maximum possible age of the molting July tower kills. (2) Fledglings probably remain near the hatching site for 20–30 days after becoming independent; 11% of all banded fledglings were observed on my study area after they became independent, and 8 of them were seen when age 61 days or older (Chapter 35). Therefore postjuvenile molt is probably complete or nearly complete before most young begin to migrate. (3) A fledgling from a nest that received egg 1 on the earliest date on which egg 1 was laid during my study (2 May) would reach age 60 days on about 15 July. Even if it then migrated immediately, it is doubtful that it would travel (about 1000 km) rapidly and directly enough to arrive in northern Florida in July. Thus, July tower kills almost certainly hatched south of my study area.

The period of nest-leaving at Bloomington (25 May–15 August) was 83 days long, the period of tower kills of immature warblers 99 days long.

Age of latest migrants: The migration of young birds continues about as late as that of adults and therefore covers a longer time span than adult migration. The evidence follows: (1) I regularly saw immatures as late into September and October as I saw adults. (2) A late migration of young is inevitable on the basis of dates of nest-leaving. Birds leaving the nest on 15 August (see p. 398) would not reach age 60 days until about 4 October. (3) The last birds killed at the Florida tower were adults, on 22, 25, and 29 October; but a young bird died on 21 October. Of the birds killed 14 October–29 October, 21% were immature, which is close to the proportion (28%) of young in the total autumn sample. (4) The last capture at Island Beach, New Jersey, was of an adult on 30 September; but two immatures were caught on 28 September.

Duration of period of migration, according to age: As expected on the basis of the preceding subsections, the migration period of immatures was longer than that of adults. Dates of tower kills of young spanned 99 days, of adults 81 days. Median dates of death were 15 September for 159 adult males, 13 September

for 132 adult females, 7 September for 35 immature males, and 3 September for 75 immature females. The sizes of the two female subsamples are more nearly alike and probably more representative of the female age structure in autumn (Chapter 38), and I therefore tested only female age classes for a difference in date. In the Mann-Whitney test (not corrected for ties), $z = 2.196$; $P = 0.028$.

Sequence of evacuation of breeding range by adults: The migration of adults probably begins in the southern part of the breeding range. Comparison of the date of the earliest tower kill of an adult, 10 August, with dates of postnuptial molt on my study area indicates that early adult tower kills could not have come from as far north as Indiana: The extreme early date of start of noticeable molt (Chapter 41) on my area was about 25 June, and the mean for the population was about 25 July. Noticeable molt lasts about 40 days, and individuals apparently do not migrate until it is complete or nearly so (see p. 444). Thus even the occasional Indiana birds that began to molt in late June would not have reached Florida by 10 August. The greatest single night of autumn mortality of Prairie Warblers at the tower was 20 August 1957 (54 adults, 15 young), pointing to large-scale departure of adults from the southern part of the range by that date. If the first migrants in Michigan, New Jersey, and Indiana were young of the year and their movement began in mid-August (p. 439), that too implies that migration of adults began earlier at southern latitudes than northern. This is consistent with the probability that breeding, having begun earlier in the south, also ended earlier there for at least some individuals.

Locations north of Bloomington, Indiana, evidently were evacuated before the Bloomington region was emptied. Of 7 adult males and 9 adult females seen in October, 14 were my banded birds; populations that had bred north of my study area apparently had already passed through. This is consistent with the fact that unbanded birds predominated among the many Prairie Warblers observed in September. If at other latitudes the last local residents to leave do so only after the regions north of them are emptied, and if southern adults begin to leave breeding locations before northern, the departure period of adults becomes progressively shorter as latitude increases. Greater synchrony of departure times, as well as times of most or all other events in the reproductive cycle, is expected in northern populations.

Sex.—The sexes probably did not differ in fall migration schedules. Extreme dates of tower kills of adult sex classes were about the same (Table 159); a median test revealed no significant difference. Six of 11 adults dying after 10 October were females; and inspection of the sex ratio of the birds killed on the 6 dates on which adult mortality was heaviest (Table 161) suggests no pattern of change according to sex and date. (Immature sex classes were not compared, because obviously the tower-killed sample is not representative for that age; see the discussion of sex ratio in Chapter 31; compare Taylor and Anderson, 1973.) Data from Island Beach, New Jersey (Table 160) suggest no schedule difference according to sex, and the result of my Mann-Whitney U-test of Murray's raw data is nonsignificant. Turning to my study area, because it was impossible to be sure that an unbanded bird was a migrant and because counts prolonged over many days might include some unbanded individuals more than once, I tabulated

TABLE 161
NUMBERS OF ADULTS KILLED IN NOCTURNAL COLLISIONS WITH A FLORIDA
TELEVISION TOWER¹ IN LARGE AUTUMN FATALITIES, ACCORDING TO SEX

Date	Prairie Warblers killed		Totals
	Males	Females	
20 August 1957	28	26	54
12-15 September 1961	14	9	23
19 September 1962	12	14	26
21 September 1963	13	5	18
25 September 1965	11	9	20
5 October 1957	14	5	19
Totals	92	68	160

¹ See pages 21 and 439 for further details; see also Nolan and Mumford (1965).

the sexes only of birds seen in October. Eleven females and eight males were seen in that month.

Museum collections (see p. 360) contain about twice as many adult males as adult females from the winter range. From August, I found 1 adult specimen of each sex; from September, 15 males and 2 females; from October, 14 males and 8 females; from November, 19 males and 7 females. The September data suggesting a tendency in adult males to arrive earlier are the only such evidence and are not convincing in view of the uniformity of the other indications to the contrary.

Date of molt.—All tower-killed birds had completed molt of flight feathers, but some were in final stages of body molt (see Chapter 41). Almost all museum specimens killed early in autumn in the winter range were in full fresh plumage. If molt is substantially completed before migration, as indicated, the further question is whether early end of molt is associated with early beginning of migration. To investigate this I classed all color-banded residents seen on my area after 15 September as late migrants and analyzed dates on which their noticeable molt was completed (as directly observed or calculated on the assumption that individuals observed during molt finished the process at the average rate). I regarded an individual as having completed molt early if its date was on or before the mean date for all color-banded birds of its sex (based on data on p. 516); otherwise it was classed as late.

In males, late migration was not associated with late molt. The mean date of completion of molt of 22 late migrants was 4 September (SD 9 days); the mean for all males was 2 September. Some late migrants finished molt quite early.

However, late migrant females probably molted late. The mean date of completion of molt of 13 late migrants was 22 September (SD 7 days); the mean date for all females was about 6 September. The earliest date of completion of molt by a late migrant was 15 September, and nine of these were still molting noticeably (two had short rectrices) when I last saw them in late September. I pursued the implications of these data by considering early migrants, i.e. females that finished reproduction by 15 August and that were observed on the study area after that date but not later than 15 September. For 10 such females, the mean date of end of molt was 2 September (SD 14 days). In a test of significance of the difference in mean molt dates of these 10 and of the late migrants, $t =$

TABLE 162
LAST OBSERVATION OF COLOR-BANDED MALES PRESENT ON STUDY AREA
IN MORE THAN 1 YEAR¹

Designation of male	Year 1	Year 2	Year 3
A	20 September	19 September	21 September
B	18 September	19 September	
C	4 October	2 October	
D	19 September	26 September	27 September
E	3 October	2 October	11 September
F	19 September	24 September	
G	20 September	25 September	
H	26 September	12 September	
I	14 September	24 September	27 July
J	27 August	3 September	20 September
K	1 September	21 September	
L	20 September	17 August	
M	18 August	25 September	
N	18 September	27 August	
O	26 August	27 September	
P	30 July	3 October	
Q	5 September	10 October	30 July

¹ See text, this page, for methods.

4.49; $df = 21$; $P < 0.001$. Again, in females there appears to have been a close relation between date of end of molt and date of departure from the study area (migration?).

Individual differences.—Only males were sufficiently site faithful to permit comparisons of final dates of observation of individuals in more than 1 year, and this comparison suggests that at least some migration schedules of individuals were consistent from year to year (compare pp. 28–29). Failure to observe a male after any particular date does not necessarily mean he had migrated or even that he had left the study area. Therefore the most probative kind of evidence of individuality would be series of unusually late sightings of the same males in more than 1 year; the assumption that migration began soon after such late observations is probably justified.

Table 162 presents dates of final sighting of all banded males (17) that bred on the area 2 or more years (1958–1962) and that in at least 1 year were seen after 1 September (see Chapter 34). Individuals are arranged from top to bottom in descending order of consistency. Of the 17, 7 (A–G) were observed in 2 or more years at very similar late dates. In at least 2 years the dates of two males (H and I) seem neither very consistent nor the opposite. The dates for the eight others (J–Q) are quite inconsistent. The October records for males C and E are especially convincing evidence of individuality, since few birds stayed so late.

WEIGHT AND FAT

Migrants from Leon County, Florida.—Mumford and I took wet weights (to 0.1 g) of intact and not obviously dehydrated tower kills from 1957 through 1967. All digestive tracts were empty. Methods and results are described in an interim report (Nolan and Mumford 1965).

Weights of tower-killed birds (Table 163) should be compared to those of

TABLE 163
WEIGHTS¹ OF AUTUMN MIGRANTS KILLED IN NOCTURNAL COLLISIONS WITH A
FLORIDA TELEVISION TOWER, ACCORDING TO SEX AND AGE

Weight	Sex-age class			
	Male		Female	
	Adult	Immature	Adult	Immature
N	149	25	110	73
Mean	8.01	8.22	7.31	7.62
SD	0.87	1.12	0.88	0.99
Extremes	10.1–6.1	10.5–6.5	10.8–5.7	10.6–6.0

¹Weights are in g. Methods are described on page 445. See also pages 18, 544–545, and Nolan and Mumford (1965).

breeding birds on my study area: 23 breeding adult males weighed a mean 7.37 g (SD 0.39 g); 41 breeding adult females weighed a mean 7.74 g (SD 0.67 g). (The greater mean weight and the greater variance of females suggest that some of these contained eggs in late stages of development.) Probably no breeding male or female had an empty digestive tract; if 0.5 g is arbitrarily subtracted from the male mean breeding weight to correct for this difference between study-area males and migrant males, the latter averaged 1.4 g heavier.

Variation associated with sex and age: It will be shown (below) that weight increased as date advanced, but this probably does not affect comparison of weights of adult males and females, because migration schedules of the sexes did not differ (see above). However, since only young birds died in July and early August, seasonal variation in weight will bias comparison of adults with immatures and cause adults to appear heavier relative to immatures.

Tests of weight differences between sex-age classes (Table 163) follow: adult male vs. adult female— $t = 6.37$, $df = 257$, $P < 0.001$; immature male vs. immature female— $t = 2.53$, $df = 97$, $P < 0.025$; adult male vs. immature male— $t = 1.07$, $df = 172$, $0.40 > P > 0.20$; adult female vs. immature female— $t = 2.22$, $df = 181$, $P < 0.05$. Clearly males were heavier than females. Almost certainly immatures outweighed adults, but the small sample of young males and the bias referred to above obscure any difference between male age classes.

Assuming that the Prairie Warbler conforms to the pattern described for other *Dendroicae* (Odum *et al.* 1964, Rogers and Odum 1964), most or all of the excess of male weight over female weight is attributable to larger overall size of males (as indicated by wing length; see Table 179). Wings of immatures are shorter than those of adults (Table 179), and obviously the greater weight of immatures cannot be similarly explained. If immature and adult migrants of equal wing length did not differ in lean dry weight (see Rogers and Odum 1964) and the nonfat body is homeostatic during migration (see Odum *et al.* 1964), it appears that migrating young Prairie Warblers are fatter than adults. Johnston and Haines (1957), weighing birds killed at a Georgia ceilometer on a single night, found evidence that immatures of certain species, including the Chestnut-sided Warbler, were heavier than adults.

Nolan and Mumford (1965) calculated wing loading (compare Clark 1971) of tower kills and discussed implications of differences among age-sex classes. Young were more heavily wing-loaded than adults and females possibly more

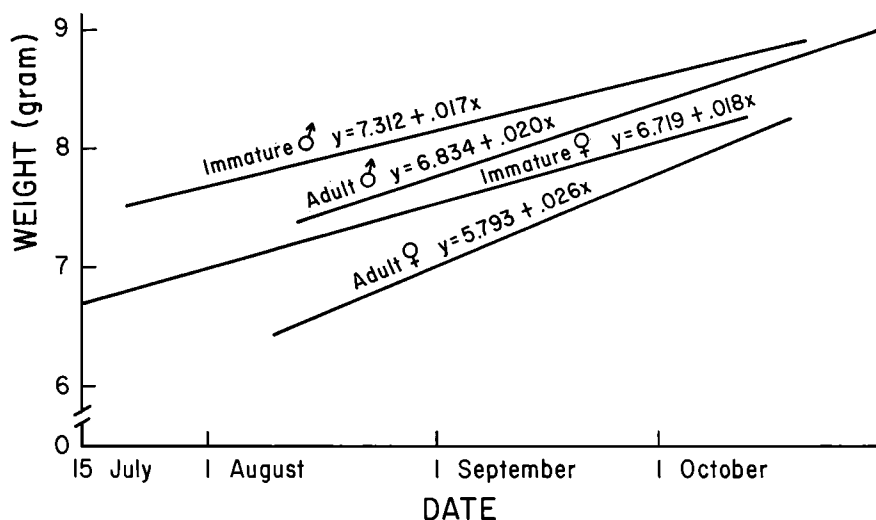


FIGURE 37. Regression of weight on date among Prairie Warblers killed during autumn nocturnal migration through Leon County, Florida, according to sex and age. Terminal points of lines indicate dates of first and last casualties. See text for data on samples.

heavily than males. Revised results to include data newly obtained follow: When mean weight of each sex-age class (Table 163) is divided by the wing area (Nolan and Mumford 1965: Table 4) appropriate to the mean wing length (Table 179) of that class, approximate loading per cm^2 of wing surface in adult males was 0.14 g; in immature males, 0.16 g; in adult females, 0.15 g; and in immature females, 0.16 g.

Variation associated with date: Regression analyses show that weights of migrants increased by about 0.02 g per day (Fig. 37). For adult males, $t = 5.28$, $df = 147$, $P < 0.001$; adult females, $t = 6.71$, $df = 108$, $P < 0.001$; immature males, $t = 1.89$, $df = 23$, $0.10 > P > 0.05$; immature females, $t = 4.15$, $df = 71$, $P < 0.001$. Wing length, therefore probably overall size, did not vary according to date (data not shown). If the weight increases were not associated with variation in overall size, and if the migrant's nonfat body is essentially homeostatic (see Odum *et al.* 1964), then the tower kills simply became progressively fatter as date advanced. Observed variation in visible fat deposits supports this view (Nolan and Mumford 1965). (Note that if the earliest tower kills came from the southern part of the range as proposed above, their lower weights cannot be associated with exhaustion of fat reserves by longer flights.)

Weights of autumn migrants of other species have been reported to rise as the season advances, but the point seems to have received little discussion (see Nisbet *et al.* 1963: 116–119; Murray 1965). Odum *et al.* (1961) reported that Bobolinks killed in October in Leon County, Florida, were consistently fatter than those killed in September and suggested that early migrants might be about to island-hop to South America, later ones about to fly nonstop across the Gulf. This possible explanation of differences in energy reserves does not readily fit the Prairie Warbler. The distance from Leon County, Florida, to the winter

range is far short of the distance ahead of the Bobolink, and the linear nature of the regression of weight on date does not suggest alternative metabolic preparations for the different routes of flight. Possibly the warbler's increase in fat permits later migrants to make fewer and/or shorter stopovers and/or enables them to cope with events imposing greater energy demands en route.

Migrants netted on Island Beach, New Jersey.—At least some of the migrants caught on Island Beach had flown out to sea at night and were returning toward the mainland; these doubtless had empty digestive tracts, but birds netted in the afternoon may have fed shortly before capture. The mean of 42 weights obtained in 1973 and supplied by Murray was 7.73 g (SD 0.88 g); extremes were 9.7 and 6.3 g. The mean for 6 adult males was 7.88 g; 17 immature males, 7.91 g (SD 0.77 g); 4 adult females, 7.68 g; and 15 immature females, 7.49 g (SD 0.96 g). Means for immature males and females, the only classes large enough to compare, do not differ significantly.

Weights of subsamples from the first and second halves of September were the same. However, many migrants caught at Island Beach have little subcutaneous fat and weigh less than migrant conspecifics from other locations, probably because the former have just made unusually long flights after being wind-drifted out to sea (Murray and Jehl 1964). Such efforts immediately prior to capture might reduce fat reserves and mask any variation normally correlated with date.

In several species, including parulids, when autumn migrants have been weighed at two widely separated locations, weights at the more southerly location have been significantly heavier (see Caldwell *et al.* 1963, Johnston 1968). Weights of Prairie Warblers on Island Beach and in Leon County, Florida (Table 163) show no such variation.

AGE CLASSES OF ATLANTIC COAST MIGRANTS

Predominance of immatures.—Fragmentary information indicates that in the Prairie Warbler, as in many other passerines, most autumn migrants observed along the Atlantic Coast are young of the year (see Robbins *et al.* 1959, Murray 1966). In 1963, at least 79% of 63 individuals caught at Island Beach, New Jersey, were immature (Table 160; see Murray 1966). In 1959, banders at that location aged 23 Prairie Warblers, 17 of which were immature; 1960 banders classed 16 individuals as immature and 1 as adult (Bertram G. Murray pers. comm.). In 1959 and 1961, J. R. Jehl, Jr. (pers. comm.) netted and skull-aged nine Prairie Warblers on or near Island Beach; all were immature. At Ocean City, Maryland, in 1959–1960, of 19 Prairie Warblers that were aged, 15 were immature (Chandler S. Robbins pers. comm.). At Monomoy, Cape Cod, Massachusetts, 31 August–8 September 1965, all of eight Prairie Warblers aged by James Baird (pers. comm.) were immature.

Among hypotheses recently reviewed by Ralph (1971) to account for the predominance of young birds among coastal passerine migrants, explanations based on inadequate sampling methods and on age-specific differences in overwater migration seem inapplicable to the Prairie Warbler. The Island Beach netting program covered the species' full migration period there and should have produced an unbiased sample, and no large overwater flight from the northeastern part of

the range is evident in the Prairie Warbler (see Drury and Keith 1962: 482). All other hypotheses suppose that most passerines observed along the Atlantic have been sidetracked from regular inland routes; coastal occurrences are therefore in essence extralimital. Hypothetical causes of such movements out of the normal range may be wind drift (see Baird and Nisbet 1960), or a greater readiness of inexperienced birds to leave safe routes, or deficient orientation mechanisms. If young fly to the coast because of inexperience, the implication is that they avoid such behavior in later years. If, on the other hand, orientation is defective, most misdirected young probably do not survive the first migration. Murray (1966: 359) has suggested, as yet another possibility, that the numbers of adults over the coast are not disproportionately low. Rather, he proposes, when wind-drifted migrants fly landward from the ocean, immatures descend on barrier beaches and are observed, whereas adults remain aloft and fly inland unnoticed.

One way to examine hypotheses that Prairie Warblers on the north Atlantic coast are outside the normal range is to compare characteristics of members of this coastal flight with characteristics of other Prairie Warblers in flights that were unquestionably beyond the range. One such undoubtedly extralimital group consists of individuals found in western United States. As will be shown in the next section, western records parallel Atlantic coast records in two important respects: (1) Almost all are associated with the autumn migration, and (2) all or nearly all individuals involved are young of the year. Therefore westward flight beyond the range and flight to the Atlantic coast may have similar causes, and the latter may indeed be extralimital. The rarity of adults in the west suggests that Murray was wrong in supposing that adults are present in representative numbers along the Atlantic coast.

To sum up, if the unquestionably extralimital cases in the west are relevant to the Atlantic coastal phenomenon, they imply that flight to and over the Atlantic is, as Ralph (1971) argues, attributable to defective mechanisms most of whose bearers are quickly eliminated by natural selection.

EXTRALIMITAL OCCURRENCES

The Prairie Warbler's range was somewhat arbitrarily defined for present purposes (compare A.O.U. Check-list 1957: 502–503, with Friedmann *et al.* 1957: 255; see Slud 1964: 326). Occurrences within a state, any part of which falls within the breeding range (e.g. Oklahoma), were ignored except for one especially informative case from an island off the coast of Maine. David Wingate (pers. comm.) finds Prairie Warblers in Bermuda so regularly that I considered occurrences there as normal and excluded them from analysis.

Most records were found in *Audubon Field Notes* and *American Birds*; others appeared in local literature. When references suggested that specimens had been collected, I corresponded to obtain details and thus was able to examine a number of specimens. I also obtained useful information from banders. Data are presented in two tables; one (Table 164) deals with individuals whose age and (usually) sex are known, the other (Table 165) with birds for which these facts are lacking.

Collected or banded birds.—Of 11 Prairie Warblers that were aged, 8 were young of the year (Table 164). The others, also young, were collected after 1

TABLE 164
PRAIRIE WARBLERS COLLECTED OR BANDED¹ OUTSIDE THE NORMAL RANGE²

Location	Date	Age ³	Sex	Additional information
Lincoln Co., Maine*	15 September 1961	Immature+	?	Caught by John S. Weske (pers. comm.)
Machias Seal Island, New Brunswick, Canada	19 August 1951	Immature#	M	Specimen GEW585, Univ. Kans. Mus. Nat. Hist.; see Woolfenden 1952
Kent Island, New Brunswick, Canada	25 August 1957	Immature#	M	Specimen 217 N.B. Mus.; see Gobeil 1968
Mid-Atlantic, 41° 37.5'N, 53° 58'W	6 September 1964	Immature+	F	In collection of Mass. Aud. Soc.; collected by Allen H. Morgan on Woods Hole Ocean. Inst. Atlan- tic II Cruise 13 (James Baird pers. comm.)
Near Ojinaga, Chi- huahua, Mexico	20 June 1959	Yearling#	F	Specimen 37905, Univ. Kans. Mus. Nat. Hist.; see Thompson 1962
Near Manzanillo, Colima, Mexico	24 December 1959	Immature ⁴	M	In collection of Allan R. Phillips; see Schaldach 1962
San Diego Co., California	23 September 1962	Immature#	?	Specimen 30296, San Diego Mus. Nat. Hist.; see McCaskie and Banks 1964
San Diego Co., California	13 October 1962	Immature#	M	Specimen 30471, San Diego Mus. Nat. Hist.; see McCaskie and Banks 1964
Volcan St. Miguel, El Salvador	15 March 1926	Yearling#	M	Specimen 17555, Univ. Cal. L.A.; see Dickey and van Rossem 1938: 495
Cocos Island, Costa Rica	26 February 1963	Yearling#	F	Specimen 789466, Am. Mus. Nat. Hist.
South Farallon Island, California*	24 September 1967	Immature+	M	Henry Robert (pers. comm.)

¹ * indicates that the bird was banded and released; all others were collected. Omitted are specimens referred to in the literature as having disappeared and lacking data on date, age, etc.; places of collection of these were within the area covered by the records in this table and Table 165.

² See page 449.

³ Age was determined by examination of the skull and/or inspection of the plumage; see Chapter 41 and Appendix 5. Birds of the year (i.e. before 1 January) are called immatures. Yearlings were collected in or after January. + indicates that the skull was examined by the bander or collector; # indicates that I examined the specimen.

⁴ "Gray auriculars, skull apparently just completing ossification" (Allan R. Phillips, pers. comm.).

January, when skulls of many individuals probably have completed ossification; but they retained traces of immature plumage (Appendix 5). Six of the 11 were males, 3 were females, and 2 were unsexed. Places of capture range from Canada to southern California, from the mid-Atlantic to Cocos Island in the Pacific.

Sight records.—Table 165 records about 50 sightings; the exact number is uncertain because the birds were unbanded and some duplication may result. Most locations at which these birds were observed fall within the area in which the 11 aged birds were found, and dates of sightings were also about the same: 41 observations were in autumn; 4, all southwest of the breeding range, were in December–February; 4 were later in spring.

TABLE 165
SIGHT RECORDS OF PRAIRIE WARBLERS OUTSIDE THE NORMAL RANGE¹

Location	Date ²	Reference
New Brunswick, Canada (9 birds)	20/8/51, 4/10/64, 25/8/66, 23/10/67, 31/10/67, 4/8/68, 26/8/69, 21/8/71 ³	David S. Christie (pers. comm. ⁴)
Cape Breton, Nova Scotia, Canada	21/9/74	Bagg and Emery 1965
Southern Texas (10 birds)	7/9/50 24/2/52, 13/2/53 2/5/62, 21/9/63, 8/8/65, 2/9/65, 17/9/67, 18/10/68, 25/4/71	Williams 1951 Goldman and Watson 1952, 1953 Webster 1962, 1964, 1966, 1968, 1969, 1971
Montreal, Quebec, Canada	30/5/66	Carleton 1966
Southern Vermont	?	A.O.U. 1957
Sheboygen Co., Wisconsin	?/5/64	Green 1964
Northern Iowa	?	A.O.U. 1957
Northeastern South Dakota	?	A.O.U. 1957
Milbank, South Dakota ⁵	7/9/61	Nero 1962
Near Tucson, Arizona	7/12/52	Phillips <i>et al.</i> 1964: 155
Various locations, California (23 birds ⁶)	3/9-4/11 ⁵	Austin 1971
Mid-Atlantic north of Puerto Rico	23/10/24	Scholander 1955 and Bent 1953: 438
Near Puerto Cabezas, Nicaragua	19/1/63	Thomas R. Howell (pers. comm.)
Mid-Pacific 12°37'N, 92°31'W	25/9/60 ⁶	Willis 1961

¹ See page 449.

² When individuals were seen on more than 1 day, only the date of first sighting is given.

³ Two individuals were seen.

⁴ One bird was aged as "adult," four as "immature"; others were not aged or age was doubtful.

⁵ Austin (1971) reports 26 California occurrences, but 3 are treated in Table 164. Sightings were in various years, and the dates therefore omit year.

⁶ Willis (pers. comm.) states that this bird, which landed aboard ship, appeared to be probably immature.

Probably all the aged birds had made a disoriented fall migration. However, those not far north of the breeding range in Maine and Canada may have been engaging in premigration dispersal, if such a movement occurs; also it is remotely possible that the Mexican and El Salvadorian specimens had made a disoriented spring flight to those countries from points in the winter range. As for the sight-recorded birds, it is clear for all but three or four that they had failed in autumn to migrate to the normal winter range.

DIURNAL BEHAVIOR

Size and composition of migrant flocks.—Most Prairie Warblers to be referred to here are assumed to have been migrating because they were associating with species that occur in southern Indiana only during migration; all were unbanded, of course. However, sometimes banded residents joined migrant parulids for a short time and acted like them (see below).

The largest aggregation of probably migrating Prairie Warblers that I saw consisted of eight that formed a loose flock; two or three was the more usual number. About 50% of such flocks included other parulids and totaled 3–20 (usually 6–10) in size; single Prairie Warblers in mixed warbler flocks were also not uncommon. Frequent associates of Prairie Warblers were Tennessee, Nashville (see

Parkes 1957), Magnolia, Black-throated Green, and Chestnut-sided Warblers. Flock organization was loose and flock membership probably temporary. For example, for 15 min I observed 6 Prairie, 2 Tennessee, and 2 Nashville Warblers that spread over an area about 20×10 m and moved along together feeding. At the end of that time some birds of the latter two species left the group.

Behavior of migrant flocks.—Typically flocks moved rather rapidly (at heights of 1–12 m, usually below 5 m) through fields and woods edge; I could keep a flock in sight 3–15 min without having to walk far, but even when I tried to follow I could rarely stay with a flock as long as 25 min.

In males, foraging was interspersed with darting, aggressive supplanting attacks and short chases, both inter- and intraspecific. Prairie Warblers were pursuers and pursued about equally often; at times they called Chek and Seep, and very occasionally males sang faintly. Positions and heights of individuals within the group changed often, and the general effect was of intense restless activity.

Occasionally single birds took off on what appeared to be long-distance flights, climbing gradually and disappearing into the distance.

Behavior of residents.—The restlessness and apparent excitement of migrant flocks seemed to be communicated to banded residents, and several times local birds temporarily joined flocks of migrant parulids and behaved as the migrants did. To illustrate, an independent banded young in September seemed to have joined a flock and was with it for 10 min, after which I lost contact. However, 6 days later the same bird was still on the study area, 700 m from the place where last seen. It associated with two flocks of migrants during about 2 hours, again behaving like these.

Hamilton (1962: 394) has suggested that flight calls of migrants overhead may stimulate birds on the ground to fly up and join them. Similarly, it seems possible that Prairie Warblers in migratory condition may be induced to begin autumn movement by joining migrant flocks, as just described, and staying with them until the home range is left behind. Lawrence (1953a: 74) discusses apparent conflict in motivation of summer resident Red-eyed Vireos that acted as though torn between remaining on the home range and joining passing migrants.

CHAPTER 37

FIDELITY TO SITES USED IN PREVIOUS YEARS

FORMS OF MALE SITE FIDELITY

The complexity of the behavior of some males requires that analysis of site fidelity consider three variables.

1. Nature of former site. A male older than 1 year could show attachment to one of the following sites of earlier years or to any combination of these: his hatching site; one or more temporary territories (Chapters 5 and 30), breeding territories, and locations occupied in the postreproductive period (Chapter 35); and sites visited during explorations (Chapter 30).

2. Interval between original use of site and subsequent expression of attachment.

3. Behavior expressing attachment. In the current year, an earlier site could serve as one or more of the following: the point toward which migration is oriented, a temporary or permanent territory, a place visited during exploration, a postreproductive site.

The descriptions that follow are organized around the last of these variables, emphasizing how behavior showed attachment to scenes of activity in past years. Table 166 summarizes the analysis.

Thirty-three color-banded males bred on the study area and returned in at least one year thereafter. These birds provide 75 cases of return following breeding in the preceding year.

Homing.—In 69 cases males were first observed, at the very beginning of the current season, on the preceding year's territory. In the period of arrival of males I inspected the entire study area daily, sometimes several times, and looked at every singer. Males sing even before reaching the breeding ground (Chapter 3), which makes them conspicuous; therefore the high proportion of initial sightings on last year's territory suggests that these birds had gone directly to it. The six males first seen other than on the former territory were on sites which became the current year's territory; they may have homed to the former site but have moved away immediately (see Chapter 5 and also the following subsection).

Some males almost certainly held two territories in succession in a single year, and a few held two concurrently (pp. 330 and 345). Many males that settled on the study area in midseason, probably having abandoned a territory elsewhere a few days earlier, came back to the study-area territory at the beginning of the next season; it is therefore reasonable to believe they had homed to the most recent territory instead of the postulated abandoned territory. Each of two males that held territories concurrently in year 1 and that returned in year 2 was first sighted on the year-1 territory that it had occupied first (earlier) in that year. However, that territory had also been the one on which reproduction had terminated later in year 1, i.e. had been more recently used.

Of males that prior to pair formation relocated from one territory to another on the study area, six returned the following year. I made special efforts to dis-

TABLE 166
FIDELITY OF BANDED MALES TO FORMER SITES, ACCORDING TO TIME
AND MANNER OF SHOWING FIDELITY

Behavior showing fidelity	Prior use of site ¹			
	Post-reproductive site	Temporary territory ³	Breeding territory earlier than immediately preceding year	Breeding territory immediately preceding year
Homing and breeding ²	0	0	0	55
Homing but not breeding ²	0	0	0	14 ⁶
Breeding but not homing	1	2	0	0
Holding temporary territory ³	0	3	1	14 ⁶
Visiting during breeding season after relocating ⁴	0	1	1	8
Returning in postreproductive period ⁵ after relocating ⁴	1	1	2	2

¹ A bird is counted once for each year it provided data.

² See pages 453–454 for the evidence of homing.

³ A temporary territory is a site defended for 1 or more days but not occupied during breeding.

⁴ See Chapter 5.

⁵ See Chapter 35.

⁶ These are the same case; after homing, males held territory temporarily.

cover such males promptly, inspecting both of their previous territories several times daily. All were first seen on the site to which they had relocated. Thus, in all cases in this and the preceding paragraph, when returning males had a choice between two or more former territories whose locations I knew, indications are that all went immediately to the more recently used breeding site.

Establishing temporary territory without pair formation.—Fourteen of the males discovered first on last year's breeding territory advertised there for 1–8 days and then left while still unmated. Another male, which in 1959 had relocated from his territory of 1958, came back to the latter in April 1960. He behaved territorially for 1 day, moved 700 m and settled for 2 days, returned and spent 2 more days on the territory of 1958, then disappeared permanently.

Some males established temporary territories on their temporary territories of previous years. Two examples illustrate the variety in these cases. (1) In April 1962, male A sang for several days on a site from which he was evicted when its former owner, male B, arrived from migration; male A acquired a breeding territory 250 m away. In 1963 and 1964, male A was first seen on his breeding territory of the preceding year but in each year he then moved to the site from which he had been evicted in 1962; male B arrived after each move and ousted male A, causing him to return to his own territory. In 1965, male A again took up male B's territory, and male B did not come back; male A retained this site from 1965 through 1967. (2) In 1960, male C behaved territorially on a site until driven from it when its former owner returned. Male C then took up a territory 500 m away and bred there for 4 years. In April 1964, he moved to the site from which he had been evicted in 1960 and held it for 2 days; he then left, apparently not as a result of any challenge by other males, and reoccupied his breeding territory of the last 4 seasons.

Establishing breeding territory.—As described in Chapter 5, in 55 cases (73%) males that returned to the most recent breeding site remained there for the season.

Some males that relocated permanently did so to the temporary territory of an earlier year. To illustrate, a male behaved territorially in a field for 2 days in April 1957 but settled 300 m away and bred there each year through 1959. In 1960, he relocated permanently to his temporary site of 1957. See also example 1 in the preceding subsection.

One male left his territory after the breeding season and settled in a different field and molted, probably staying in this postbreeding site until migration. He relocated to that site in the following spring and bred there for two seasons.

Visiting during breeding season.—The following examples indicate that sometimes, possibly often, exploring males (Chapter 30) visited locations they had occupied in earlier years. (1) A male relocated his territory immediately after returning in spring. Later in the same season he visited the abandoned territory, approached the incubating mate of the current territory owner, and was attacked by the owner. Instead of being routed immediately as is usual for trespassers, the explorer fought back for 10 min, the behavior of the two males sometimes resembling circular pursuit (see Chapter 6). The explorer then left; he was not seen until he made another exploration to the same territory early next year. (2) In May, a male visited a territory abandoned 2 years earlier. (3) After relocating, six males were seen briefly (mid-April to mid-July) on the territory of the preceding year. One of these explorations was 1.5 km from the territory of the current year.

Exploring males also visited their temporary territories of other years.

Occupying and visiting after reproduction.—About 30% of the males left current territories when the breeding season ended (see Chapter 35). Two were then seen on the territory of the preceding season; one of these visited that territory and then disappeared, but the other probably remained until he migrated.

Three males went to territories on which they had bred more than 1 year previously, as the following shows. (1) A male left a territory when all shrubs and trees on it were cut down in July 1958, and he was not seen again until he returned to the site in August and September 1960; by that date the field was again shrub-covered. (2) In 1959, a male abandoned his territory of 1958 and left the study area. In 1960, he relocated back to the study area but not to his 1958 territory; thus he probably held at least three breeding territories in 3 years. He disappeared on 29 July 1960, deserting nestlings, and was seen on 15 September on his territory of 1958, 1.5 km distant from the 1960 territory; he returned to the 1960 territory 3 days later.

MALE RATE OF RETURN IN SUBSEQUENT YEARS

Methods; characteristics of sample.—A "return" is a reappearance on the study area, however brief, by a male that had nested there the preceding year. The sample on which the return rate is based consists of 55 color-banded individuals; at least 9 were yearlings when they first bred on the area, and the rest were of unknown age. Because all or most males that relocated to new territories probably homed to them, as described above, any male that disappeared from the study area after returning in spring is excluded from calculations involving years subsequent to his disappearance. This is true even for those that were seen on the

TABLE 167
RATES OF RETURN¹ BY BANDED BIRDS BREEDING ON STUDY AREA

Years returned	Males (55 banded)		Females (105 banded)	
	N	%	N	%
First year	33/55	60	20/105	19
Second year	20/28	71	11/20	55
Third year	12/18	67	4/11 ²	36
Fourth year	8/9	89	3/4	75
Fifth year	4/6	67	1/3	33
Sixth year	0/3	0	0/1	0

¹ Definitions of return differed for the sexes; see pages 455 and 458. Methods are described on pages 455-456.

² One female that returned in the first, second, and fourth years is treated as having returned in the third although she was not seen.

area in subsequent years, unless they relocated back to the study area; see the related material, page 465, for further details. These exclusions account for variations between size of the numerator in some fractions in Table 167 and size of the denominator in the fraction showing return rate in the immediately following year.

Two preliminary questions arise about the reliability of the data: (1) Is error introduced by the small size of the study area? Animals with strong site fidelity might confine their movements to a tract as large as, say, 20 ha; if Prairie Warblers had done this, I would probably have failed to see many that returned. (2) Considering that at least 27% of males relocated shortly after arriving in spring, how great is the possibility that some moved away before I had a chance to learn of their return?

The following facts respond to both questions and lead to the conclusion that the estimate of the return rate will be approximately accurate. (1) About 65% of the males that bred were observed in later years, a percentage so high in comparison with survival data for other temperate zone passerines (e.g. see Farner 1955: 416-417) that it is most improbable that any substantial number of additional survivors went unobserved by me. (2) The large proportion of returned males first sighted on the most recent breeding territory indicates that attachment, expressed by homing, was to an area of 1-3 ha (Chapter 29 reports territory sizes). This permitted efficient and reliable data collection. (3) Only one male was found after having gone unseen for a year, and he had left the study area when his territory had been completely cut over. All other males were seen in runs of consecutive years, always immediately after arrival in April. Had any significant number moved before I found them, or had coverage of the area been inefficient, erratic observation dates and gaps in sightings would be expected.

Results and discussion.—Of the 55 males, 33 (60%) returned in the year following first breeding on the area while banded. In later years the rates were greater (Table 167), an increase that is probably the result of sampling error. It should be noted that attachment to a specific territory did not grow stronger with time; males often relocated after occupying a territory several years (see Table 5). Such relocations are ignored in Table 167, which deals only with fidelity to the breeding site of the year before. Although von Haartman (1949:

TABLE 168
FIDELITY OF BANDED FEMALES TO FORMER BREEDING SITES, ACCORDING
TO TIME AND MANNER OF SHOWING FIDELITY

Year site was last used ¹	Behavior showing fidelity		
	Homing but not breeding	Homing and breeding	Occupying or visiting after breeding
Immediately preceding year	9 ²	13	3
Earlier year	1 ³	1(?) ³	3

¹ A bird is counted once for each year it provided data.

² In 14 additional cases females were first seen at a site not known to have been used in an earlier year.

³ The breeding site of the immediately preceding year was not on the study area and was unknown; possibly the female homed to it before reappearing on the study area.

26) interpreted results somewhat similar to those in Table 167 as possibly the result of "decreasing mortality" in Pied Flycatchers, his sample and the increase in his return rates were larger than mine. Further, his rates of first, second, and third return were below 50%; a genuine increase in survival with age is not beyond reasonable expectation when the return rate is so much lower than the Prairie Warbler's initial return rate of 60%.

If the annual rate did not change significantly with age, all fractions in Table 167 can be pooled and a rate obtained from the larger numbers; of 119 cases, banded males that bred on the study area returned 77 times (65%). There is independent evidence (Chapter 38) that 65% of the breeding population consisted of birds older than 1 year, and I therefore conclude that essentially all surviving males returned to the most recent breeding site or its immediate vicinity.

FORMS OF FEMALE SITE FIDELITY

This section is organized like the comparable section for males, and methods are the same. Table 168 summarizes the data.

Homing.—In 22 of 36 cases (61%) a female was first seen on the territory of her last mate of the preceding season. In most instances for which there is information, these females had also spent the postbreeding period there, a point considered to be important (see p. 461). Nine of the 22 left the study area (3 never to be seen again) shortly after being sighted in April or May; they probably bred elsewhere. Considering that females were much less conspicuous than males and that they changed location more often (Chapters 30 and 31), the high percentage of initial sightings at last year's breeding site suggests that those that returned homed as precisely as did males. (As the following section shows, many females that survived did not return at all.)

Fourteen females were first seen at sites other than those they were known to have used in earlier years. Two then disappeared; the rest nested on the area but at locations they had not occupied previously, at least not while banded. Most of these 14 were first observed within 100 m of the preceding year's breeding site, but one was about 2.3 km from it.

One female appeared early in 2 seasons at a breeding site she had occupied 2 and 3 years ago, respectively, and in each case disappeared for the remainder of the season.

Establishing temporary home range without breeding.—Most females that moved did so immediately, probably the day they arrived from migration. The following is an exception: In 1960 and 1961, a female settled for 4 and 5 days, respectively, on her 1959 breeding site and associated with a different territorial male each year but did not nest. The following subsection reports this female's later history.

Breeding.—Fourteen females nested on a home range overlapping the most recent breeding home range of the preceding year. Distances between last nest of the earlier year and first nest in the year of return ranged from 12 to 325 m (mean 90 m). Identity of the mates of these birds, i.e. whether they had also been their mates formerly, is discussed on pages 98–99.

The female whose case is detailed in the preceding subsection returned in 1962 to her 1959 site and this time remained to breed with the fourth male she had associated with there in 4 years.

Occupying or visiting after reproduction.—In July or August three females appeared on the breeding site of the preceding year and remained throughout molt and probably until migration. One of these had the following history: She was banded in 1957 on a breeding home range 1 ha in area. She came back to it and molted in the postreproductive periods of 1958, 1959, and 1960, presumably having bred off the study area. In 1961, she nested on the study area 500 m from her 1957 breeding site (her perennial postreproductive site) to which she returned when 1961 breeding ended.

FEMALE RATE OF RETURN IN SUBSEQUENT YEARS

Methods; characteristics of sample.—"Return" is any reappearance on the area by a female that had been seen on it in the preceding year and had bred on it at least once. This definition is less restrictive than that for males (p. 455); to include only females that had nested on the area in the immediately preceding year would reduce the sample too drastically. The looser standard could produce a biased low estimate of the rate of second and subsequent returns, but the fact that females changed breeding sites more than did males has a compensating tendency. That is, the more frequent movement by females increases the likelihood that an individual that relocated to a site off the study area would come back to the study area and be observed again. That coverage of the area was efficient is indicated by the following: Only 1 of 20 females that returned at least once reappeared after having gone unobserved an entire year; 11 were seen at least 3 straight years after the year of banding, 1 of these in 5 straight years.

The sample consists of 105 individuals, 4 banded as nestlings and the rest as adults (20 yearlings, 51 old birds, remainder not aged).

Results.—Following a low initial return rate of 19% there was a striking rise in second returns, to 55% (Table 167). Rates for third and later returns are based on very small samples; if these are pooled the rate following second return is 42%. In short, if a female came back once, the probability that she would do so again was almost as high as in males; in a test of independence, the data on second returns for the sexes do not differ.

TABLE 169
SITE FIDELITY OF CALCULATED SURVIVORS¹ OF 105 FEMALES,² ACCORDING
TO REPRODUCTIVE RESULTS³ IN YEAR BANDED⁴

Result of reproduction	Number in year of banding	Calculated survivors next year	Returned	Survivors returning, ⁵ %
Successful	53	34	16	47
Unsuccessful	36	23	4	17
Unknown	16	10	0	0
Totals	105	67	20	—

¹ Adult annual mortality was 35% (Chapter 38).

² Females were caught without considering their ages; the sample is probably representative of the population's female age structure.

³ Success is the production of at least one young Prairie Warbler or Brown-headed Cowbird that left the nest.

⁴ Included are four birds banded as nestlings; for these, results of the reproductive effort in the first year of breeding on the area is shown.

⁵ Percentages are based on calculated numbers of survivors.

These results are much like those reported by von Haartman (1949: 21–31) for female Pied Flycatchers in Finland: 11% returned in the year after banding (as compared to 37% for males), but 54% and 60%, respectively, made second and third returns (see also Löhrl 1957: 176). Possibly more significant because a parulid is involved, Walkinshaw (1953) found that 50% of male Prothonotary Warblers returned, whereas only 12 (20%) of 59 females returned in the year following banding; but 6 of those 12 then came back next year (compare Hann 1937: 152–153; Mayfield 1960: 204–205).

Clearly, the data on returns of female Prairie Warblers are more complex than those for males, and the following sections investigate this problem.

Variation in fidelity according to postbreeding location in year preceding return.

—As described in Chapter 35, I made diligent searches for 54 banded females that nested on the study area and were still present at the end of breeding; and I found 23 in the postreproductive period. (A few females present in more than 1 year were counted more than once.) Of those 23, 14 (61%) returned the following year. The adult annual mortality rate was about 35% (Chapter 38); evidently all or nearly all survivors of the 23 females found on the area after breeding came back to it. Of the 31 females that were not found, 6 (19%) returned next year; this figure is 30% of the 20 survivors that would be expected on the basis of a 35% mortality rate. In a test of independence of the return data for the 23 and 31 females adj. Chi-square = 8.1; df = 1; $P < 0.005$.

The foregoing evidence of an association between fidelity to the area after breeding and fidelity the following spring is reinforced by an almost identical result when the somewhat overlapping data for all 105 banded females are considered: 23 were seen after reproduction in the year of banding, and 15 (65%) of those 23 were among the 20 females that returned at least once (Table 167). The individuals in this paragraph and the cases discussed above both numbered 23 by coincidence.

Variation in fidelity according to success of reproduction in preceding year.—Of the 105 banded females, 53 nested successfully (defined on p. 385) in the summer when banded and 36 did not; for 16, results are unknown. The number of successful females expected to be alive the following spring is 34 and of unsuccessful fe-

TABLE 170
RETURNS OF FEMALES, ACCORDING TO WHETHER REPRODUCTION WAS
SUCCESSFUL¹ IN PRECEDING YEAR

Reproductive result in year of return	Females	Number returning in following year
First return (20)		
Successful	7	6
Unsuccessful	6	1
Unknown	7	4
Second return (11)		
Successful	5	2
Unsuccessful	3	0
Unknown	3	2
Third return (4) ²		
Successful	0	0
Unsuccessful	1	0
Unknown	3	3
Fourth return (3)		
Successful	0	0
Unsuccessful	3	1
Unknown	0	0

¹ Success is the production of at least one Prairie Warbler or Brown-headed Cowbird fledgling that left the nest.

² One female that returned in the first, second, and fourth year is treated as having returned in the third although she was not seen.

males 23, assuming no relationship between reproductive success and subsequent mortality. As Table 169 shows, 16 successful females (47% of the calculated survivors) returned and 4 unsuccessful females (17%) did so. In a test of independence, adj. Chi-square = 4.1; df = 1; $P < 0.05$. If individuals are counted as separate cases each year they were present, and returns of successful and unsuccessful females following each summer of success or failure are considered, $P < 0.025$. In this test no allowance was made for calculated mortality.

The greater tendency of successful nesters to return is evident even when attention is confined to the few females (20) that returned at least once. Table 170 presents (1) numbers of these that succeeded and failed in the year of first return; (2) numbers that made a second return, according to whether they had succeeded or failed the preceding season; and (3) these facts for still later returns. The samples, though small, indicate that even among the little group of females that were faithful to the study tract an individual that returned but failed to bring off young was less likely to come back next year. Pooling the data in Table 170, following 12 successes were 8 returns (67%), following 13 failures 2 returns (15%). In a test of independence, adj. Chi-square = 4.9; df = 1; $P < 0.05$.

Two collateral points: (1) Among an expected 34 surviving successful females, only 16 returned. Therefore about 18 moved elsewhere. (2) Previous reproductive success and return were not associated in males. Of 55 cases in which males succeeded, 33 (60%) returned; of 29 unsuccessful males, 19 (66%) returned.

Returns in year 2 by female Pied Flycatchers apparently were significantly affected by failure to reproduce in year 1, i.e. the summer in which they were

first studied (von Haartman 1949: 40–41; see also Coulson 1972). However, all but one female flycatcher left her mate's territory immediately after nest loss; this is so unlike the most common reaction (re nesting) of female Prairie Warblers after nest loss that the parallel in behavior of the two species in the following spring may be fortuitous.

Other possible associations.—Tests for an association between age and return by females suggested no relationship.

No field evidence suggested that the higher rate of second and subsequent returns was the result of exclusion of inexperienced females by more experienced birds; females rarely fought (Chapter 31). In any event, mathematical considerations based on the age structure of females (Chapter 38) eliminate the possibility that inexperienced females bred elsewhere. The rise in rate of second returns cannot be explained as stemming from a survival rate improving with age; there is no evidence of such improvement (see Chapter 38).

Finally, von Haartman's (1949: 21–41) hypothesis of polymorphism to explain differential site fidelity of female Pied Flycatchers cannot be applied to the Prairie Warbler. Site-faithful females showed no tendency to have site-faithful daughters, and most females that returned to their hatching site on the study area were progeny of mothers that had not shown site fidelity.

A HYPOTHESIS CONCERNING FEMALE SITE FIDELITY

Statement.—An explanation fitting the foregoing facts is that most or all surviving females returned in spring to the postbreeding site of the preceding year and paired near that spot if courted by a suitable male. The positive correlation between reproductive success and return can be accounted for thus: Success of early nests was low; and females replaced nests often, sometimes after a change of mates, until they brought off young or passed out of reproductive condition (see Chapters 33 and 34). Assuming two females that began to build the final nest of the season on 25 June, the one whose nest failed, say on 10 July, would immediately be free to leave the study area; in this situation females almost always did leave. The one that succeeded (on about 21 July) would probably stay in the general vicinity of the nest site until about the end of the period of dependence of her young on approximately 22 August (Chapter 28). Meanwhile this latter female's molt would be arrested, to begin or resume approximately when her parental duties were ending (Chapter 41). During molt she would tend to be less active (Chapter 35) and therefore would probably continue on the area.

Under this hypothesis the effect of success on site attachment is indirect. Any factor(s) determining location in the postreproductive period, when attachment hypothetically arises, is equally effective. A genetically based mechanism contributing to return to the scene of successful reproduction and avoidance of the site of failure, if this behavior were adaptive, would be selected whether it operated directly or indirectly. The hypothesis also proposes breeding locations for the many surviving females that never returned to the study area. These birds cannot be ignored or simply dismissed as lacking site fidelity; it is not probable

that their northward migration the following spring had no goal (see Howard 1960; see also Brewer and Harrison 1975).

The suggestion that the target of the female's spring migrations might change from year to year is consistent with the evidence that the male's goal changed after he had relocated his territory.

Additional data.—(1) The mean date of end of reproduction (nest failure or independence of young) of 30 females that I did not find in the postbreeding period and whose dates of breeding I knew is 22.5 July (SD 18.2 days); for the 21 females that I found and whose dates of breeding I knew, the mean is 11.7 August (SD 17.8 days). In a test of significance, $t = 3.94$; $df = 49$; $P < 0.001$.

(2) Each of the two samples just referred to contained 16 successful females. The mean date for attainment of independence by fledglings of birds not seen in the postreproductive period is 30.3 July (SD 21.9 days); the corresponding date for birds present in the postreproductive period is 19.1 August (SD 12.4 days); $t = 3.15$; $df = 30$; $P < 0.005$. Thus, it was not simply success but success at a late date that was associated with presence on the study area after breeding.

(3) In 17 cases I knew the date at which a female's reproduction ended, found her on the study area after breeding, and saw her again next year. In 11 of these 17 the females succeeded, 9 of them after 14 July and all after 24 June; 1 bird had succeeded at an early date but on 20 July lost a second-brood nest; 5 failed altogether. If the female whose second-brood attempt failed is excluded because her case is ambiguous, 32% of the other 16 birds produced no fledglings, a figure close to the estimate of unsuccessful females in the population as a whole (41%; see Table 133). This reinforces the view that site fidelity was not directly linked to success. As to the five females that were unsuccessful but nevertheless returned next year, one quit breeding on the area on 10 June, one on 1 July, but after she had begun to molt, and three after 21 July. The bird whose nest failed on 10 June probably paired again (Chapter 34), possibly near the study area.

(4) Of the six females that I did not find after breeding ended and that returned next year, four had brought off young after 25 June. Therefore some or all of these adults probably remained near the study area until late July or thereafter; note the movements of some females with fledglings described in Chapter 28. If any females remained nearby, their cases are not evidence against the proposed hypothesis.

(5) Several episodes, trivial in themselves, provide suggestive support. To illustrate, a female banded as a nestling appeared on the study area after the breeding season of her first adult year, 600 m from her hatching site. Next spring she returned and nested at about the spot where I had seen her late in the preceding summer.

(6) Females breeding on the study area after second and subsequent seasons were no more successful in reproducing than old females not known to have bred there before and no more successful than yearling (i.e. inexperienced) females (Table 171).

TABLE 171
REPRODUCTIVE SUCCESS¹ OF FEMALES, ACCORDING TO BREEDING EXPERIENCE
ON STUDY AREA IN PREVIOUS YEARS

	Cases	Successful	
		N	%
Old, nested on study area in previous year(s)	24	12	50
Old, not known to have nested on study area in previous year(s)	37	18	49
Yearlings	24	13	54

¹ Reproductive success is the production of at least one Prairie Warbler or Brown-headed Cowbird that left the nest.

RETURNS BY BIRDS PRODUCED ON STUDY AREA

Three males and 7 females that hatched on the study area were seen as adults, 9 of them when yearlings; 4 returned in more than 1 adult year. Dates at which this site-faithful group had left their nests covered the full period of nest-leaving and were distributed representatively, with six cases falling on or after 14 July (see p. 398).

Six of the 10 returnees nested on the study area as yearlings, another not until her second adult year. Two males had territories 2.6 and 2.9 km distant from the hatching site. Four females built first nests about 100–800 m from the hatching site (mean 450 m). The female that did not nest on the area as a yearling appeared briefly in August of her first adult year and returned next season to the same spot and nested 600 m from her hatching site. Only the two males bred on the area in more than 1 year, one of them three times and one twice.

Three of the 10 never nested on the study area. One of these, a female, was seen only once, nearly 3 years after hatching. Another female spent 1 week, in August after her first postnuptial molt, at her hatching site. A male appeared 700 m from his hatching site in late July of his first adult summer and was seen again in the following April, 1.2 km from his hatching site.

Rate of return.—Ignoring mortality between nest-leaving and 30 April of the first breeding season (Chapter 38), the rate of return of fledglings was about 4% (10 of 272 color-banded individuals that left the nest). The sex ratio at nest-leaving appeared equal (Chapter 31); if it was, 2% of male and 5% of female fledglings returned. Assuming mortality rates discussed in Chapter 38, 87 of the 272 banded fledglings survived until 30 April of the yearling year. If all 10 birds seen on the study area are treated as having returned as yearlings, return of the calculated survivors was 11%. Finally, if the sex ratio was at unity at all relevant times, 7% of calculated surviving males and 16% of females returned (compare Berger and Radabaugh 1968). Note that the latter figure is about the same as the rate of first return of females banded as adults.

As von Haartman (1949: 29–30) implies, the mechanism causing a young bird to return to its hatching site cannot be assumed to be identical with the mechanism that brings an adult to the site of earlier adult activity. Unlike the

case of adults, evidence does not suggest that yearling warblers homed to a site as small as a territory. The return rate in this age class makes it more probable that in the initial spring migration young birds oriented toward some more general area in which the hatching site lay. Nevertheless, if distribution of returnees was random throughout this postulated target area, the calculated 11% return rate to a tract the size of my study area would indicate that the target of migrating yearlings was not large.

CHAPTER 38

SURVIVAL AND MORTALITY; POPULATION STRUCTURE

ANNUAL SURVIVAL RATE OF ADULT MALES

Methods.—Probably all surviving old males returned to the territory of the preceding year (Chapter 37), permitting dynamic analysis of their survival (see Hickey 1952: 3–12; Farner 1955: 400). Cases are both pooled without respect to year and segregated into annual subsamples. The pooled composite will produce a reliable estimate only if annual mortality was constant or varied normally around a long-term mean. The data show that this condition probably was met (see discussions on pp. 467 and 468–469).

The sample is 53 males (banded 1955–1962) whose territories I inspected until 1970, more than 3 years after the last one had been seen. In the first year of breeding on the study area, nine of these were known yearlings, either banded as nestlings or showing traces of the first nonnuptial plumage; the others were of unknown age. In the latter group, yearlings undoubtedly were more numerous than in the breeding population generally, because by 1958 most arriving males had been banded in earlier years and I tried to catch only the unbanded birds.

Adjustments caused by relocation of territories: Analysis is complicated by relocations of some males either soon after arriving or in midseason. Because the new territory evidently became the target of spring migration the following year, males that relocated to sites off the study area cannot be used for calculation of survival in the year following relocation. This is true even of those males that I saw sometime after the year had ended; to include these as survivors and to exclude from the sample all other males that had relocated would bias the calculations in favor of survival. The same reasoning requires exclusion of individuals that relocated to new territories on the study area; the latter were found because they survived. However, males whose new territories I discovered reentered the sample one year after the relocation, if alive then; they were used in the survival calculation for the 12 months following reentry.

Dates of annual survival period: Survival is analyzed for the period 1 May–30 April. However, a few banded males returned and relocated before 30 April, and a few males breeding on the area for the first time did not appear until shortly after 1 May; observations between 25 April and 5 May are considered equivalent to those on 1 May. For example, a banded male that returned 20 April and disappeared 5 days later is counted as having survived to 30 April.

Most unbanded males holding territory for the first time were caught in May or early June; between 1 May and date of banding, identity is assumed because of continuities in behavior.

Terms: In analyzing the composite sample and ignoring calendar years, the year a banded bird first bred on the area is “year x ”; the following is year $x+1$, etc. Correspondingly, survival periods (1 May–30 April) are “period y ,” period $y+1$,

TABLE 172
ANNUAL SURVIVAL¹ RATE OF 53 ADULT MALES² IN YEARS FOLLOWING YEAR
OF BANDING

Years after year of banding	Surviving males	
	N/N alive 1 year previously (maximum N possible) ³	%
1	30/53	57
2	17/21	81
3	11/16	69
4	6/7	86
5	4/6	67
6	0/3	0

¹ Survival is measured from 1 May to 30 April.

² Nine males were yearlings in the first year they bred on the study area; the rest were of unknown age, but see page 465.

³ See pages 465–466 for methods.

etc. "Total number banded" is the full sample of 53. "Annual number banded" excludes any males that relocated in the year of banding. The survival rate for each period is determined from the number of males present at its end, expressed as a percentage of the "maximum number possible" to be present. For period y , the maximum number possible is 53. For period $y+1$ the maximum number possible is the number present at the end of period y , adjusted by subtracting males that relocated during $y+1$. Calculations for period $y+2$ and later periods proceeded the same, except that males that prior to the beginning of the period had relocated to a territory on the study area were added to the maximum number possible, as explained above. "Number returned" includes all males from the maximum number possible that were present at the end of the period whose survival rate is being calculated.

Results and discussion.—Survival in period y was 57%, in $y+1$ 81%, and in all subsequent periods pooled 66% (Table 172; compare Hickey 1952: Table 51). For almost all bird species studied to date, the adult annual survival rate appears not to change with advancing age, until samples are too reduced to be reliable (e.g. Hickey 1952, Lack 1954: 97–98, Farner 1955; see also Palmer 1962: 14–15). The difference in rates in Table 172 for periods y and $y+1$ raises the question whether male Prairie Warblers departed from this common avian pattern. I believe they did not, but the following possibilities must be considered.

(1) If being banded or wearing bands before becoming accustomed to them increased mortality, survival in period y would be lower than in $y+1$. However, I injured no male; and daily observation of males, usually for at least several weeks after banding, did not suggest that wearing bands handicapped them. (2) If the higher mortality characteristic of juveniles (e.g. Hickey 1952, Farner 1955) continued to affect males between ages 1 and 2 years, survival would be lower in period y . But such a "prolonged period of juvenile mortality" (Farner 1955: 418) appears to be known only in some nonpasserines whose maturity is delayed. Lack and Farner (see Farner 1955: 403) agree that stabilization of annual mortality rate occurs by 1 January of the year following hatching in north temperate-zone passerines. (3) It is theoretically possible that survival in period y was not low but rather that in period $y+1$ it was higher than during other seg-

TABLE 173
ADULT MALES Banded, ACCORDING TO YEAR, AND NUMBERS SURVIVING¹
INTO SUBSEQUENT YEARS

Males banded, by year (Total N = 53)	Males returning/maximum number possible, ² by year													Total
	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	
1955 (N = 2)	2/2	1/1	0/0											
1956 (N = 3)		1/3	0/0											
1957 (N = 8)			7/8	6/7	2/5	1/1	0/1							
1958 (N = 14)				8/14	3/5	2/3	0/1							
1959 (N = 6)					3/6	2/2	3/3	2/2	2/2	0/2				
1960 (N = 13)						5/13	2/3	2/2	2/2	1/2	0/0			
1961 (N = 2)							1/2	1/1	1/1	0/0				
1962 (N = 5)								3/5	2/2	1/2	1/1	1/1	0/1	
Totals														
N	2/2	2/4	7/8	14/21	8/16	10/19	6/10	8/10	7/7	2/6	1/1	1/1	0/1	68/106
%	100	50	88	67	50	53	60	80	100	33	100	100	0	64

¹ Survival calculations are based on the period 1 May–30 April. For methods, see page 465.

² See definitions on pages 465–466.

ments of adult life. This is improbable. Nothing observed in the field would lead me to expect such increased survival. Further, the maximum number possible for period $y+1$ consisted of males of various ages, which almost eliminates any age-specific survival factor as the cause of a real increase in the $y+1$ rate. Finally, Chi-square is nonsignificant even when only data for periods y and $y+1$ are tested for independence, a biased test because it selects the numbers most likely to show a difference.

I therefore conclude that the adult male annual mortality rate was probably the same for all survival periods, i.e. despite increasing age. If so, each period for which a male provided data can be treated as independent and all periods pooled to form a larger sample: From a maximum number possible of 106, the number returned is 68 (64%). While not entirely independent of these data, sample sizes of males selected for analysis of age-related variation in the pre-pair formation period were 56 old (64%) and 31 yearling (36%) (Chapter 11). And in samples selected for comparing territory size according to age (Chapter 29), 47 males were old (67%) and 23 yearlings (33%).

Table 173 presents survival data by calendar year; it groups males without regard to number of previous years they had been present, because of the conclusion reached in the preceding paragraph. No long-term trend in the survival rate is suggested; note that the highest rates were for 1957–58 and 1963–64. The 95%-confidence limits of each subsample include 64%; hence all could have been drawn from the same binomially distributed population. Although in that population survival could in theory have remained the same through the years, it probably varied normally around a long-term mean (see von Haartman 1951: 13). If so, the sample rates in Table 173 combine both genuine fluctuation and sampling error. As stated earlier, this belief that survival rates probably varied normally is the justification for pooling data across calendar years to obtain a mean rate. See also the discussion of population stability over time, in connection with the survival rate of adult females (pp. 468–469).

ANNUAL SURVIVAL RATE OF ADULT FEMALES

Because of the lesser site fidelity of females (Chapter 37), survival data are meager. However, time-specific analysis (see Hickey 1952: 3–12) is possible, since old and yearling females can be reliably aged by plumage (Chapter 41). Age structure will reflect the survival rate, assuming population size did not change over time. Consideration of the validity of this assumption is deferred until the data are presented.

Observed survival.—Restricting consideration to females that displayed site fidelity, 11 of 20 individuals (55%) returned in year $x+2$ (see Table 167 and the discussion in Chapter 37). Pooling data on female returns as was done for males, at least 19 of 39 (49%) survived from 1 May to 30 April. Females were less able than males to breed at the sites they preferred (p. 36), and because they were less conspicuous than males they were more likely to be overlooked by me if they passed through the study area without breeding. Therefore a known survival rate of 49% is impressively high and suggests that females in fact survived as well as males. A test of independence of the composite return data shows no difference between the sexes. This result is expected, because the sex ratio appeared balanced at all ages for which there was information (Chapter 31).

Population structure.—Of 166 females that nested on the Griffey Tract (1958–1964) and that I examined in the hand, 108 (65%) were old and 58 (35%) were yearlings. Of 60 museum specimens of adult females collected in the breeding range between 1 May and 31 July (see p. 360 for the museums), 36 were old (60%) and 24 yearlings (40%).

Annual age ratios of breeding females follow, with only numbers and percentages of old birds shown: 1958—25 (61%); 1959—14 (59%); 1960—14 (56%); 1961—12 (60%); 1962—18 (75%); 1963—14 (87%); 1964—11 (69%). The 95%-confidence interval of each annual subsample includes 65%; i.e. the variation is no greater than expected in successive samples of the same binomially distributed population. In a test of independence of size of age classes and year Chi-square is nonsignificant ($P > 0.25$).

The assumption that the population was either constant or that it fluctuated about a mean (see Deevey 1947: 288, Farner 1955: 405) must now be considered. Although breeding pairs declined steadily in fields in which succession was not disturbed by fire and cutting (from 16 in 1958 to 10 in 1965), this does not invalidate the assumption if (a) the study-area population was part of and subjected to the dynamics of some larger regional population at equilibrium, and (b) females had no age-specific preferences for or aversions to the area. I believe these two conditions were met, because of the following evidence: (1) The population was not self-contained, and an interchange of breeding birds within a larger region was clearly evident. Movements of adults to and from the study area and sometimes back again were numerous (Chapter 37; see also pp. 32, 35, 344, 349, 434). (2) Few yearling females that bred on the area had been produced there. Yet a significant correlation existed between annual production of fledglings for the years for which there are sufficient data (1957–1962) and percentage of breeding yearling females in the respective following years; $r_s = 0.83$;

$P \cong 0.05$ (see data in preceding paragraph and Table 146). Because most of these latter yearlings were produced off the area, this result could be coincidence. But much more likely, production on the study area was a representative sample of production in the region that supplied most yearling breeders to the area (see p. 463). In that event, high study-area production in year 1 reflects a regional condition and accounts for numerous 1-year-old breeders in year 2. (3) Clearly, successional changes caused the dwindling in number of settlers on the study area each year, producing a process like emigration. This population decline was not paralleled by annual decreases in adult male survival, or in production of fledglings, or in proportion of yearling females breeding. And even as breeding pairs on the area declined, newly abandoned fields adjoining it were colonized and their populations rapidly increased. A peripheral part of the area itself, abandoned by Prairie Warblers after a fire, was recolonized at the time the undisturbed fields were losing breeders. Therefore the population of the region could have been at equilibrium; and the annual rates of male survival, production, and proportion of yearlings suggest that it was. (4) The last-mentioned rates make it very unlikely that any age class preferred or avoided the study area or was excluded from it by other age classes.

In sum, study-area females probably are an unbiased sample of a larger population whose age structure reflects, in part, annual survival rate. The pooled rate for all adult females (65%) could, of course, conceal unequal rates at different ages. However, this is unlikely; the survival data for males and the smaller sample for females both indicate a rate unvarying with age. I shall therefore use 65% as the annual survival rate for both sexes of adults (for rates of other parulids, see Farner 1955: 436, Mayfield 1960: 204–206, Anderson and Maxfield 1967, Roberts 1971, Diamond and Smith 1973).

DISTRIBUTION OF ADULT DEATHS DURING YEAR

Probably very few adults died on the study area. There was no sign of starvation and little of disease (see below). Two nesting females were probably killed by predators (see p. 412), the only evidence of predation on adults. These females had nests in sample 2 (p. 397). The median active life of 300 nests observed throughout their active lives was 11.4 days, suggesting a death ratio of 2 females in 3420 days of what may have been the most vulnerable part of the season for either sex. For subsequent calculations, I conjecture a study-area death rate of 1% per month. At that estimate, 5–6% of the adult population died on the breeding ground and only 14–17% of all annual mortality fell in the spring-summer months. This is consistent with the “widely held view that bird populations are primarily regulated by mortality outside the breeding season” (Krebs 1970: 324).

SURVIVAL OF EGGS AND NESTLINGS

Egg and nestling survival are analyzed in Chapter 33. See also the complete life table below (Table 174).

SURVIVAL OF FLEDGLINGS

Survival from nest-leaving to independence, a period lasting about 32 days, is estimated from information on 87 color-banded young in 36 family units (see p. 309). I searched for these fledglings approximately daily (1952–1962) from the time they left the nest until survivors became independent. Methods used to meet problems caused by movements of family units are identical with those described in Chapter 28, with two exceptions: (1) If an entire unit including the parent disappeared simultaneously before the young were 40 days old, I excluded the case from the sample. (2) If the parent continued to be observed while all young in the unit disappeared prior to age 33 days, they were considered dead; if disappearance of the young was at age 34–35 days, the case was excluded from the sample; if disappearance was at age 36 days or older, young were treated as having survived.

Of the 87 fledglings, 71 (82%) survived. No tendency appeared for survival to vary according to family-unit size of one to three fledglings; but, as discussed on page 321, I saw no case in which one adult brought four young to independence. Loss of the care of one parent was probably very dangerous to members of broods of four and five.

The data do not reveal how deaths were distributed during the period, but certain mortality factors probably were most severe at its beginning, when young were least adept at movement.

SURVIVAL BETWEEN INDEPENDENCE AND FIRST BREEDING SEASON

Data on annual production, survival during dependence, and percentage of yearling breeders can be used to calculate survival from independence to breeding, provided that the study-area population was a representative sample of the surrounding region. It is critical that fledglings produced on the area and unbanded yearlings breeding there next year have been members of a single population subject to the same dynamics; this subject has been discussed above in connection with annual survival of adult females.

For convenience, calculations will be related to the calendar: Mean date of termination of dependence is taken as 15 August (see p. 398 and Chapter 28), 16 August as the beginning of independence.

Number of fledglings produced per 100 adults was 108 (Table 133). A death rate of 18% (above) reduced this to 89 fledglings on 16 August, by which date the assumed adult death rate would have diminished the 100 adults to 96, a ratio of 1.00 adults to 0.93 immatures. On the following 30 April–1 May, 65 survivors of the original 100 adults would be present; this survival rate since 16 August (8.5 months) is 68%. If population size were stable, 35 yearlings would also be present from the 89 immatures of the preceding 16 August; survival between independence and return on 30 April–1 May, then, is estimated at 39%. The adult-to-yearling ratio would now be 1.00:0.54.

A crosscheck of this calculation against productivity (see Hickey 1952, esp. Table 6; Farner 1955: 407) is impossible, because productivity was used in the calculation. Intuitively, if 68% of adults survived the period 16 August–1 May, a 39% rate for young birds in the same period seems to me "of a reasonable order"

(Farner 1955: 407). It would not be unexpected if about twice as many young (61%) die in their first 8.5 months of independence as do adults (32%) in that same period.

The only potential source of information about the distribution of these deaths is the age composition of museum specimens, which I analyzed. No pattern was detected.

MORTALITY FACTORS AND DANGERS, FROM NEST-LEAVING ONWARD

Disease.—Of about 725 adult females (live, museum skins, and migrants killed in Leon County, Florida), 6 had what appeared to be *Poxvirus avium* foot lesions. Five of these females were breeding on my study area. Among males, 2 of about 600 had foot lesions. Both affected males were migrants killed in Florida. Observed symptoms on birds of both sexes included loss of digits and shortening of claws, regarded as almost certain indications of pox (Katherine A. Goodpasture pers. comm.); some individuals had pinkish, knobby or lobed protuberances on the tarsometatarsi and pinkish discoloration and/or swellings on the toes. Karstad (1971) lists parulids, including a *Dendroica*, as sufferers from foot pox.

A male museum specimen (AMNH 178701) has a knob-like protuberance at the base of the bill, a site often attacked by avian pox (Karstad 1971).

The case of a banded female, first studied in 1957, is of interest. In her third season, pinkish areas on her right foot were noticed on 24 June 1959; she avoided using that foot and occasionally took weight off it by perching with her belly resting on a branch. By 28 June areas on the right foot, and by 1 July some toes on both feet, were swollen. On 5 July she perched normally and the swellings seemed smaller. She was not observed again until 19 May 1961. Her left foot lacked the hallux, and all other left toes were short stubs; the right foot looked normal. She rarely or never perched on thin branches and often selected limbs large enough to permit her to lower her belly and rest her body. She also fluttered her wings frequently to maintain balance and bobbed her tail exaggeratedly. This female paired and built at least two nests in 1961 and fed nestlings until their destruction by a predator.

Three of the five study-area cases occurred in late July, 1958, which suggests an outbreak of infection (see Karstad 1971).

Mites.—Parasitic (or possibly parasitic) mites were found in 23 warbler nests; details of some cases have been reported (Nolan 1955, 1959b). The mites were *Ornithonyssus sylviarum* (Canestrini and Fanzago): Dermanyssidae; *Cheyletia* sp.: Cheyletidae; *Trombicula alfreddugesi* (Oudemans): Trombiculidae; *Oribatula* subgenus *Zygoribatula* sp.: Oribatulidae; Analgeroidea: Analgesidae. Of these, *Ornithonyssus*, *Trombicula*, and Analgeroidea were almost certainly bird parasites; I have no information about the others.

Ornithonyssus, perhaps the most injurious of the listed species (Boyd 1951, Benbrook 1965: 944), probably parasitizes warblers of all ages; it was present in great numbers in a few nests. Adults appeared to pick at and eat these mites (see Chapters 22 and 25; Boyd 1951). Several 6-day-old nestlings from nests containing many apparent *Ornithonyssus* had blood or scabs on the tarsi (but see reference to chiggers, below).

Trombicula alfreddugesi, a chigger, has been reported as parasitic on the Prairie Warbler (Wharton and Fuller 1952: 131). Boyd (1951) states that trombiculids are blood-suckers and attack birds' feet; chiggers cause dermatitis in some birds (Wharton and Fuller 1952: 131). Benbrook (1965: 945) mentions "itching vesicles or even abscesses" and "[a]pparently a toxemia. . . ."

Boyd (1951) reports that analgesids and related families derive all nourishment from feathers, mostly ventral feathers of the alar tract (see also Baker and Wharton 1955: 379-380).

Mites found on bodies of migrant Prairie Warblers killed in Leon County, Florida, are reported in Nolan and Mumford (1965). Among them were the nasal mite *Ptilonyssus*. Nasal mites can injure chicks and may play a role in ornithosis (Baker and Wharton 1952: 81; but see Benbrook 1965: 951-952).

Ticks.—Nolan and Mumford (1965; see also Peters 1936) recovered the tick *Haemaphysalis leporispalustris* Packard from a migrant Prairie Warbler. Ticks can cause loss of blood sufficient to be fatal to birds (Benbrook 1965: 952). Lowered production in fowl is associated with blood lost to ticks but possibly also with tick-produced toxic substances. "Ticks in general are notorious transmitters of other parasites" (see also Boyd 1951: 367).

Lice.—Two male warblers collected near my study area carried the feather lice *Menacanthus* sp. and *Ricinus* sp. (determined by Dr. K. C. Emerson). Nolan and Mumford (1965) report additional lice taken from migrants. Geist (1931) collected *Ricinus pallens* (Kellogg) from a Prairie Warbler in Ohio, Peters (1936) from a Maryland specimen. Of the lice mentioned, Menoponidae and Ricinidae suck blood and serum and eat feathers, while Philopteridae are feather feeders (see Boyd 1951). According to Turner (1971), severe infestations of lice irritate and cause excessive scratching, anemia, and possibly other blood conditions, and may so damage feathers that the victim appears almost to be molting (compare Keymer *et al.* 1962). A banded male Prairie Warbler on the study area lost most feathers of the upper throat and chin in early June, long before molt would be expected; the probable difficulty of delousing the throat and chin suggests that lice may have been responsible.

Nematodes.—Mumford and I found several nematodes in the abdominal cavity of an adult male and one in the pectoral muscle of an adult female, both killed in Leon County, Florida. An accident destroyed these specimens before they could be determined.

Dangers associated with migration.—As long-range migrants flying partly over water, some Prairie Warblers must die from exhaustion and in accidents (see Wetmore 1926: 121 *et seq.*). Death probably occurs even in favorable weather; Hill (1957) reported landing of exhausted Prairie Warblers on his ship in the Florida Straits during mild, normal weather (see p. 23).

Chapter 36 reports data on Prairie Warblers found outside the range and others seen in winter far north of the winter range. Extralimital birds that survive probably do not return to the breeding population; most must die quickly, some by flying out to sea and others by starving. Paul Slud, who collected a Prairie Warbler on Cocos Island in the Pacific Ocean off Central America, regarded conditions there as so unsuitable that the bird would probably have starved (*pers. comm.*). Data in Chapter 36 imply that mortality from deficient migration is nearly limited to the first

autumn and winter of life, doubtless contributing to the lower survival rate at that age. Most Prairie Warblers found in the United States in winter must starve.

Nocturnal migrants may rarely collide with trees, but in recent times fatal collisions with buildings have become more than occasional freak accidents (see Merriam 1885; Bonhote 1901, 1903; Overing 1937; Spofford 1949; Johnston and Haines 1957; Nolan and Mumford 1965).

Other accidents.—Prairie Warblers may collide with obstacles under circumstances other than migration, as suggested by Tiemeier's (1941) discovery that 4.5% (1.8% of a small subsample of parulids) of over 6000 bird skeletons showed healed bone injuries. Warblers engaging in melees (p. 50) or fleeing from predators might hit branches, and some clumsy landings of fledglings are little more than collisions with limbs in the line of flight. Tiemeier (1941) believes injured immature birds are much less likely to survive accidents than are adults, suggesting another cause of greater mortality at that age.

I observed the following: (1) a migrant male whose very crooked right tarsus evidently had broken about 1 cm above the base of the toes and had healed; (2) a banded territorial male that temporarily lost the ability to fly more than 2–3 m (see p. 41); (3) a banded male one of whose wings drooped considerably in late August but was held normally 2 weeks later (he returned next year); (4) a migrant male with bloodstains on the left side.

The behavior of two females whose wings were injured in netting accidents suggested a stereotyped cryptic reaction to inability to fly. One female moved along the ground into a very small clump of grasses and dead branches and become so immobile, probably under a branch, that I could not find her; I saw her several weeks later. The other darted to a tuft of grass and crouched at its base. When I walked up, she moved to my foot and tried to crawl under it, circling it closely several times and repeatedly attempting to get beneath it.

Hawks.—Hawks (species are named on p. 416) sometimes flew over carrying items resembling birds, and I twice observed predation on adult passerines: An American Kestrel caught a male cowbird feeding on the ground, and a Cooper's Hawk ate a freshly caught Brown Thrasher. Most male Prairie Warblers continued to sing and ignored hawks flying nearby; one sang while a kestrel called loudly overhead. However, males sometimes froze at sight of hawks. One, advertising before most trees had leafed out, crouched when a Broad-winged Hawk soared in his direction, then flew 6 m into the nearest leafed-out tree and perched motionlessly for 1 min near the trunk.

Owls.—Warblers probably occasionally fell prey to Screech and possibly Great Horned Owls (see Allen 1924, Eynon 1952). In a film by Allen H. Morgan (presented at the 1959 meeting of the Wilson Ornithological Society) Prairie Warblers erected the crown feathers near a tethered Screech Owl. I saw a pair mobbing a Screech Owl, and a mounted Screech Owl that I presented to several warblers sometimes elicited crown raising and once gaping.

Snakes.—Rat Snakes and Racers must occasionally catch fledglings, considering that I was able to approach young up to age 12–13 days and to seize them with a sudden movement. I observed a Racer with a live, still unharmed Field Sparrow recently out of the nest; I can imagine no reason why young warblers would be less vulnerable. A Racer entered a trap and ate a 10-day-old cowbird and a

warbler fledgling I had placed there; another appeared to try to get into a trap containing fledglings.

Prairie Warblers joined other species in mobs, but usually it was impossible to know whether they were reacting directly to the predator or to the behavior of the mob itself. Of 18 mobbings (14 April–28 July) 6 certainly and 5 others probably were directed at snakes; some were caused by me.

Starvation.—Evidence of starvation was lacking after the age of nest-leaving, but adults could surely starve during spells of cold, wet weather such as sometimes occur in Indiana in mid-April (see Chapter 4). Dependent young that became separated from their parents could starve; I saw apparently untended fledglings that called steadily as though hungry.

In view of the opinion "that starvation outside the breeding season is much the most important density-dependent factor in wild birds" (Lack 1966: 280), it seems worth speculating whether the great expansion of the warbler's population in the past century might now tax food resources in the winter range. Danforth (1931: 94) reports the Prairie Warbler as quite common in Puerto Rico in most years, "but some years it is very rare. In the winter of 1928–29 it was extremely scarce." The simplest hypothesis to explain large reductions in numbers in Puerto Rico is mortality there, unless the winter population of the island also breeds as a discrete population and suffered losses or low production on the breeding ground in 1928.

Exposure.—Death of fledglings from exposure probably was not common; I looked for newly fledged young following heavy night rains and usually found them in good condition. Once a storm probably accelerated nest-leaving by one day and the youngest fledgling, wet and chilled, died the following morning.

Eye disorders.—Seven times adults kept one eye closed while behaving normally in other ways; usually they had recovered within 1 day. But a male had his right eye closed whenever I saw him from 2 July through 10 July; by 14 July it was open.

POPULATION STRUCTURE AND SURVIVORSHIP

Methods.—This section presents a synthetic complete life table; the data for each age class are composite (see Deevey 1947, Hickey 1952, Farner 1955, Southwood 1966: Chapter 10). Early life is divided into biologically meaningful developmental stages, and survival is therefore analyzed over unequal intervals (compare Paynter 1966: 500). Because survival of eggs and nestlings is known to the day, the table uses time units of 1 day or multiples thereof. Hickey's view (1952: 13, 5–7; see also Deevey 1947: 309) that "[i]n theory a life table ought to start with the zygote" is followed as closely as possible; the table begins at laying.

In addition to the foregoing, other calculations are presented to facilitate comparison with data for other species. These calculations include (1) expectation of further life in years (Farner 1955: 400); (2) age in units of deviation from mean length of life (Deevey 1947: esp. 288); (3) survivorship based on an abridged life table (not shown) in which 0 age is the beginning of life as an adult; and (4) abridged survivorship for the interval from laying to nest-leaving. In the abridgment for adult life, 0 age is 311 days, which is the mean age of

yearlings on 1 May (based on 15 August as the end of dependence; see p. 470); mean expectation of further life of yearlings alive on 1 May is the mean life span while adult. The cohort is then reduced annually by the adult average annual mortality rate, 35%, and survivorship is plotted by converting each year of adult life into a percentage-unit of deviation from the mean.

Table 174 presents numbers of individuals alive between each two age intervals (L_x) calculated by

$$L_x = \frac{(l_x) + (l_x + 1)}{2}.$$

Prior to age 311 days, the table cannot be used to calculate population structure at a point in time, because early stages of development tended to be date-specific; i.e. there are very few fledglings in May, very few eggs in August.

Laying until nest-leaving: The data consist of an estimated 1107 eggs from sample 2 (p. 397); distribution of dates of laying is representative, and the sample covers 9 years (both University Farm and Griffey Tract). In two respects the data differ slightly from the sample 2 data analyzed in Chapter 33: (1) Nests in which no eggs were laid are irrelevant and were ignored. (2) I took into consideration here, and not in Chapter 33, that females whose nests were destroyed during laying probably laid the egg that was in the oviduct at the time of nest destruction; this added an assumed 15 dumped eggs to those laid in nests.

Nests too high to see into were assigned the modal clutch size for the date. Disappearances (deaths) of nest contents between inspections on successive days were attributed to the later day. Time of death of eggs that failed to hatch was estimated from appearance of the contents when I opened these eggs; deaths of apparently undeveloped eggs were divided equally between days 1 and 2 of incubation. Dumped eggs were regarded as having died before incubation began. Unless their color had revealed them as dead (p. 176), eggs taken by predators were assumed to have been alive.

Each day started at 0000. All eggs of a clutch were assigned the same age for two reasons: (1) Approximations in the data would make it illusory to try to achieve complete accuracy by calculating each day's egg as 24 hours younger than its predecessor. (2) All individuals of a clutch were probably at about the same stage of development, because of the timing of beginning of incubation (see Chapter 21). The latter fact, in turn, suggests that onset of regular incubation be taken as age 0; but that is unsatisfactory because pre-incubation losses caused by cowbirds and predators were important and should be reflected in the table. As a compromise, the table originates with laying of egg 1 but treats the laying interval as 0.5 days long for all eggs in the clutch. Thus an egg dying during the laying interval lived 0.25 days, one surviving through day 1 of incubation lived 1.5 days; death during day 1 was at age 1.0 days. Each subsequent day is treated similarly (see left-hand column of Table 174) until nest-leaving; the fledgling is regarded as 21 days old at that point. Lengths of subsequent age intervals are multiples of 1 day.

For purposes of these calculations the incubation period and nestling interval are standardized as, respectively, 12 days (ending at 2400 on hatching day) and 8 days (ending at 2400 of the last full day in the nest).

TABLE 174
COMPLETE SYNTHETIC¹ LIFE TABLE FOR PRAIRIE WARBLER POPULATION
OF STUDY AREA

Age in days (x) ²	Age as % deviation from mean length of life (x') ³	N surviving at beginning of age interval out of 1000 eggs laid (l _x)	N dying in age interval out of 1000 eggs laid (d _x)	N alive during age interval (L _x)	Mortality rate per 1000 alive at beginning of age interval (1000 q _x)	Expectation of life remaining for individuals of age x ⁴ (e _x)	
						Days	Years
0-0.5	-100.0	1000.0	187.6	906.2	187.60	86.1	0.24
0.5-1.5	- 99.4	812.4	84.5	770.2	104.00	105.3	0.29
1.5-2.5	- 98.3	727.9	65.8	695.0	90.15	116.4	0.32
2.5-3.5	- 97.1	662.1	39.7	642.3	59.97	127.0	0.35
3.5-4.5	- 95.9	622.4	68.2	588.3	109.57	134.3	0.37
4.5-5.5	- 94.8	554.2	25.9	541.3	46.73	149.5	0.41
5.5-6.5	- 93.6	528.3	37.1	509.8	70.26	155.8	0.43
6.5-7.5	- 92.5	491.2	36.3	473.1	73.81	166.5	0.46
7.5-8.5	- 91.3	454.9	32.8	438.5	72.11	178.7	0.49
8.5-9.5	- 90.1	422.1	21.6	411.3	51.12	191.6	0.53
9.5-10.5	- 89.0	400.5	42.3	379.4	105.60	200.9	0.55
10.5-11.5	- 87.8	358.2	21.6	347.4	60.24	223.8	0.61
11.5-12.5	- 86.6	336.6	38.8	317.2	115.38	236.9	0.65
12.5-13.5	- 85.5	297.8	16.4	289.6	55.07	266.7	0.73
13.5-14.5	- 84.3	281.4	27.6	267.6	98.16	281.2	0.77
14.5-15.5	- 83.2	253.8	11.2	248.2	44.22	310.7	0.85
15.5-16.5	- 82.0	242.6	12.9	236.2	53.38	324.0	0.89
16.5-17.5	- 80.8	229.7	16.4	221.5	71.43	341.2	0.93
17.5-18.5	- 79.7	213.3	18.1	204.3	85.02	366.4	1.00
18.5-19.5	- 78.5	195.2	11.2	189.6	57.52	399.3	1.09
19.5-20.5	- 77.4	184.0	16.4	175.8	89.20	422.6	1.16
20.5- 52	- 76.2	167.6	30.8	152.2	184.00	462.9	1.27
53- 310	- 38.4	136.8	83.4	95.1	610.00	531.5	1.46
311- 675	+ 361.2	53.4	18.7	44.1	350.00	902.2	2.47
676-1040	+ 785.1	34.7	12.1	28.7	350.00	897.8	2.46
1041-1405	+1209.1	22.6	7.9	18.7	350.00	888.7	2.43
1406-1770	+1633.0	14.7	5.1	12.2	350.00	876.1	2.40
1771-2135	+2056.9	9.6	3.4	7.9	350.00	852.7	2.34
2136-2500	+2480.8	6.2	2.2	5.1	350.00	827.6	2.27
2501-2865	+2904.8	4.0	1.4	3.3	350.00	789.6	2.60
2866-3230	+3328.7	2.6	0.9	2.2	350.00	724.4	1.98
3231-3595	+3752.6	1.7	0.6	1.4	350.00	619.5	1.70
3596-3960	+4176.5	1.1	0.4	0.9	350.00	465.3	1.27
3961-4325	+4600	0.7	0.7	0.4	350.00	233.0	0.64

¹ The data used to calculate mortality rates are composite. See text.

² The text relates age intervals in days to stages of development, the adult annual cycle, and date.

³ Mean length of life from the zygote is 86.1 days. Deviations are calculated from the beginning of each age interval.

⁴ Expectations are calculated from the beginning of each age interval.

Daily mortality rates of eggs and nestlings differ somewhat from those in Chapter 33 and without explanation might be thought inconsistent: (1) Some samples analyzed in Chapter 33, e.g. those showing stage-specific nest failure, were different than the sample analyzed here. (2) Treatment of samples in Chapter 33 and here differs considerably, e.g. in length of laying interval. (3) Chapter 33 analyzes nest failures and within-brood losses separately, whereas Table 174 pools them.

Dependence after nest-leaving: This period is standardized at 32 days, beginning with the day of nest-leaving. Although deaths of fledglings probably were most numerous soon after nest-leaving, evidence of this is lacking. I therefore assumed a random distribution; mean point of death is the end of the 16th day.

Independence until return as yearlings: The interval 16 August–30 April (see p. 470) lasted 258 days. Again, in the absence of evidence that deaths were non-randomly distributed, individuals dying during the period were treated as having survived one-half of it, viz. 129 days.

Adult 12-month survival periods: Table 174 applies the 35% adult mortality rate. Because of the probably uneven distribution of deaths during the year, the formula (Deevey 1947: 284)

$$e_x = \frac{T_x}{l_x}$$

is not used in calculating expectation of further life. Instead, as of each 1 May the period of survival of birds that died in the ensuing year is taken as 233 days. This was obtained as follows: The 1 individual per 100 assumed to have died in May lived 15 days, the 1 in June 45 days, etc; the last of 5 deaths on the study area is assigned to 15 September. All remaining birds that died survived 153 days on the breeding ground (1 May–30 September); if they died, on the average, halfway between 1 October–30 April, they had lived 259 days since (including) 1 May. The mean survival of the 35 adults per 100 that died is 233 days.

Results.—General characteristics of survivorship: The survival curve in Figure 38, summarizing Table 174, is Deevey's or Pearl's Type III (Deevey 1947: 285–286) and Slobodkin's Type IV (1962: 35); it is positively skewed rectangular. Few individuals survive immaturity, but those that do have a rather high expectation of further life: Only about 5.3% of 1000 would remain alive at age 311 days, but the last of these would not die for many years (see below).

Figure 38 may approximate Deevey's Type-III theoretical curve more closely than any yet reported for a bird (see Deevey 1947: 309–310; but see Paynter 1966: 502–503). Deevey's conclusion (*op. cit.*: 298) that "it may well be true that the theoretical curve, in its most extreme form, is not to be looked for among terrestrial vertebrates" may have been influenced by the biased method of estimating nest success accepted at the date he wrote (see Mayfield 1960: 188; 1961; see also p. 378).

Mean longevity: Newly laid eggs had an expectation of further life of about 86 days, or 0.24 years (Table 174), the estimated mean longevity of the cohort. Taking 15 August as the end of dependence and treating the young bird as then 52 days old (laying interval plus incubation period plus period of dependence after hatching), it would reach age 86 days about 18 September.

The number of the original cohort that would survive to age 86 days can be calculated as follows: On the day that age would be attained, 13% of the age interval 53–310 days would have elapsed. If deaths were distributed randomly, 13% of the 83 individuals to die during the age interval would be dead by age 86 days; the 137 that had been alive at the beginning of the age interval would be reduced to 126 at the point of mean longevity. Yearlings surviving to age 310 days, on 30 April, would have lived 360% of the mean life span of the cohort.

For comparisons of my data with data on other birds, a prescribed initial date (see Farner 1955: 399) can be used. Expectation of further life at various ages (Table 174) are, of course, equivalents of mean longevity from and after those same ages; the beginning of an age interval can be used as a prescribed initial date.

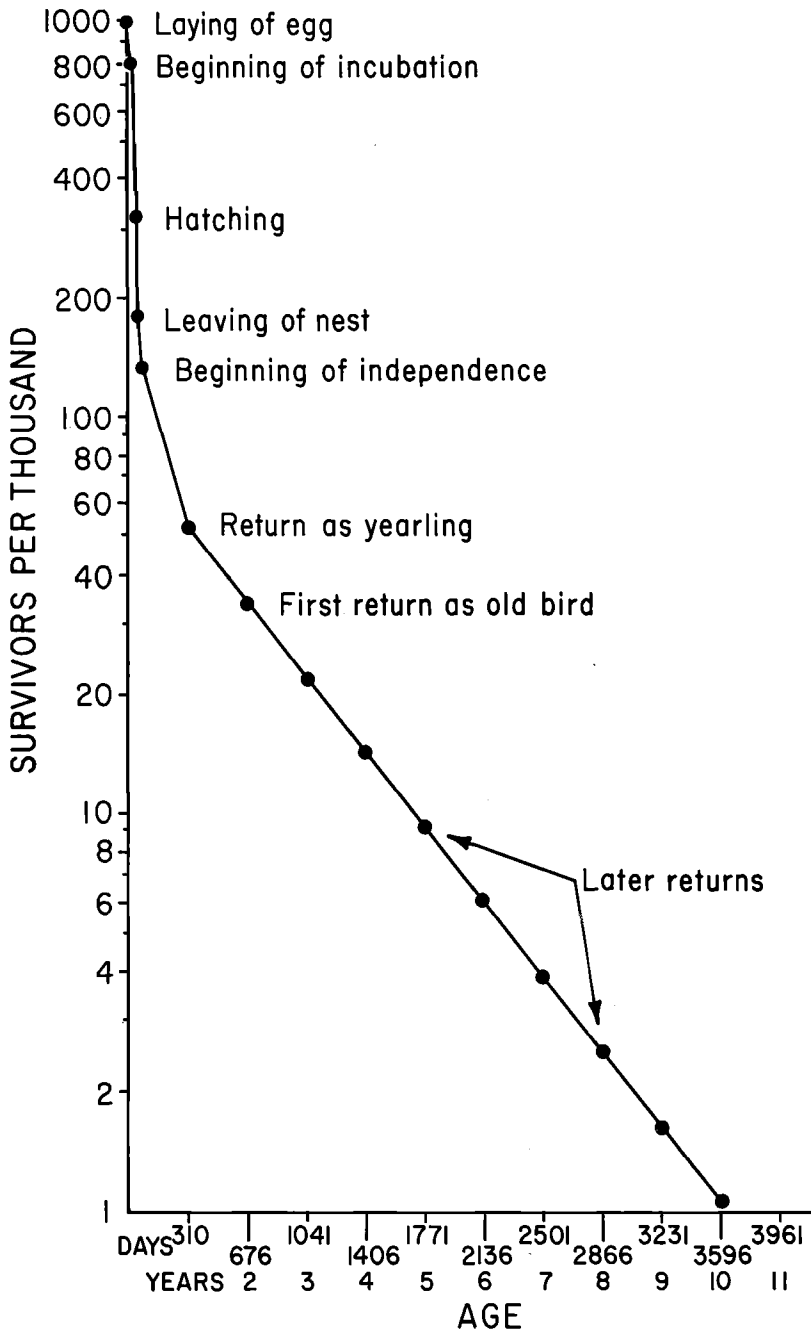


FIGURE 38. Complete survivorship curve of 1000 Prairie Warblers, from the laying of the eggs. The first 310 days of life are on a slightly enlarged scale on the X axis. See text and Table 174.

On the first full day of independence (16 August) expectation of further life or mean remaining longevity is 1.46 years; next 1 May it is at its maximum, 2.47 years. (As indicated on p. 477, these are calculated directly from the life table. If Farner's 1955: 409 formula 5 is used and mean survival in the year of death taken as 233 days, expectation of further life on 1 May of the first adult year is 2.50 years.) After 1 May of the first year the expectation decreases, as is characteristic when the annual mortality rate is constant (Southwood 1966: 285–286).

Certain authors (see Farner 1955: 403, 410) have used the first 1 January of life as the prescribed initial date for abridged life tables. By linear interpolation between expectations at ages 53 days (16 August) and 311 days (1 May), on 1 January expectation of further life of young Prairie Warblers is 1.99 years, or 728 days.

Mean longevity of 2.47 years from the initial 1 May of life is greater than that calculated for most passerines (see Farner 1955: 435–438, Mayfield 1960: 206). The 35% annual mortality rate of the Prairie Warblers studied may be unusually low for a temperate-zone passerine (see Lack 1954: Chapter 9, Farner 1955: 435–438; but see more recent survival studies, e.g. Roberts 1971, Nisbet and Medway 1972, Diamond and Smith 1973; compare Snow 1962: 96–98).

Potential natural longevity: The last survivor of 1000 eggs would die at age 3828 days, or 10.5 years (Table 174), assuming application of the 35% mortality rate to birds of advanced age and survival of 233 days beyond (including) 1 May by the 1.1 bird alive at age 3596 days (see Farner 1955: 399; Deevey 1947: 310–311). The oldest Prairie Warblers I observed in nature were 3 males and 1 female banded as adults and studied for 5 years, exclusive of the year of banding. The female was not a yearling when banded and therefore was at least slightly over 7 years old when last seen (compare Diamond and Smith 1973: Table 1). Kennard (1975) reports recovery of a banded male Prairie Warbler whose minimum age, estimated from dates of banding and recovery, was 10 years, 3 months. A female Black-and-white Warbler was killed about 11 years after she had been banded at an unspecified age (Blake and Cadbury 1969), and a male Kirtland's Warbler lived at least 9 years (Mayfield 1960: 206; see also Hann 1948).

Relation of mean to maximum longevity: When mean longevity is 86 days, the individual's expectancy is that it will live 2.3% of the potential natural life span of 3828 days. Or, the last survivor will live 4446% of the mean longevity of the group (Table 174). "[T]he ratio of the maximum to the mean approaches . . . infinity for Type III" survival curves (Deevey 1947: 310).

Comparing mortality patterns of various bird species in terms of deviation from mean longevity as of the beginning of adult life, Deevey (1947: 292) discovered that the adult survival curve "has a slope corresponding to a mortality of about 320 per thousand per 100 per cent deviation. If . . . this line [is] projected, it cuts the age axis at about +560 per cent, implying that if the mortality of birds is really constant throughout life, the oldest bird in a group of 1000 adults should survive about 6.6 times as long as the average bird." Graphs accompanying this statement indicate that Deevey intended to say "survival of about 320," etc. If I am correct in this view, Figure 39 reveals that the Prairie Warbler population conformed almost exactly to Deevey's proposition.

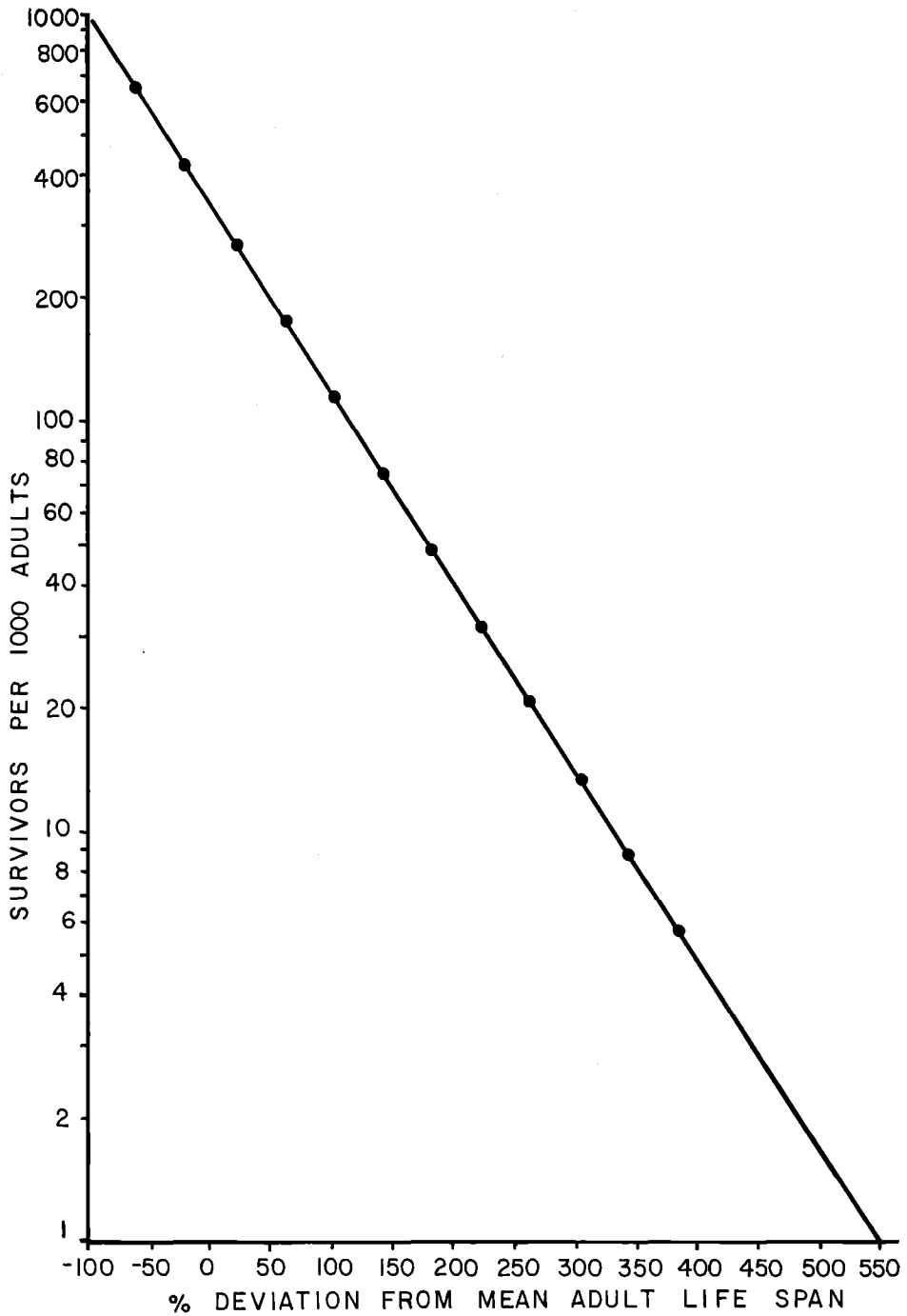


FIGURE 39. Abridged survivorship curve of 1000 adult Prairie Warblers, with age expressed in units of deviation from expectation of further life (i.e. adult life span = 2.47 years) on 1 May of the first adult year. See text.

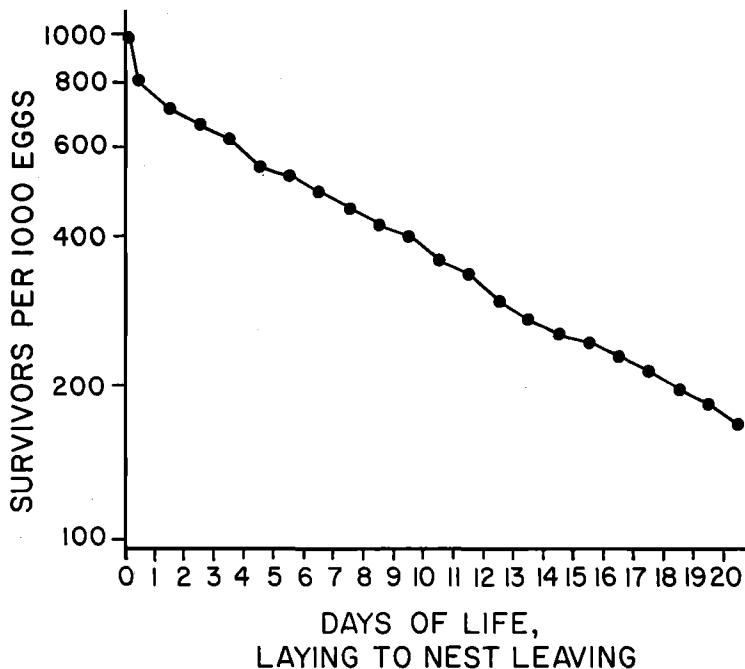


FIGURE 40. Abridged survivorship curve of 1000 Prairie Warblers, from laying of the eggs until leaving the nest. See pages 475-476 and Table 174.

Survivorship of eggs and nestlings: Figure 40 plots survivorship data (Table 174) during the 20.5 days of nest life. After an initial dip attributable to heavy mortality during laying, the curve becomes the straight-line type (Type II of Deevey 1947: 285; Type III of Slobodkin 1962: 35). Daily rates in Table 174 (excluding age 0-0.5 days) fluctuate, but not sufficiently to affect the straightness of the line on a logarithmic plot, particularly because much of the fluctuation is probably random. This line's shape does not necessarily imply absence of significant variation in daily mortality rates during nest life (compare Deevey 1947: 295); as reported in Chapter 33, daily rates probably did vary in the population studied.

THE POSSIBILITY OF POPULATION REGULATION

If the population in the region surrounding Bloomington fluctuated around a mean, as proposed, most would attribute this to processes in some sense density-dependent (see Solomon 1958, Varley 1958). The steady, emigration-like decrease of Prairie Warblers on the study area eliminated any possibility of finding statistical relationships between annual breeding numbers and other processes that affect population level (see Varley and Gradwell 1968; Krebs 1970).

However, the annual ratios of old to yearling females are suggestive of runs of nonrandom change over the years (1958-1964) for which I have useful data. When annual percentages of old females present are converted from numbers (p. 468) to signs showing direction of each year's change relative to the

preceding year, these were -, -, +, +, +, -. Annual survival percentages of males (Table 173) for the same calendar years from which the female data were taken, also converted to signs, were -, -, +, +, +, +. These also suggest runs and—more striking—runs paralleling (but nonsignificantly) changes in female age structure. If there were indeed parallel nonrandom annual changes in adult mortality rate and percentage of old birds breeding, these changes would likely be reflected in similarly nonrandom variation in population level. This in turn could imply regulation (see MacArthur 1958: 601–602).

The significant positive correlation (see p. 468) between annual production of fledglings and next year's percentage of breeding yearling females leads to the question whether fledgling production was also correlated with male survival rate. A negative correlation might suggest density-dependent forces operating (not necessarily exclusively) on adults outside the breeding season. Data are available for only six pairs of years: 1957–1962 for production (Table 146) and 1958–1963 for survival rate of males (Table 173). Spearman's rank correlation coefficient (0.60) is nonsignificant in a one-tailed test. Rankings for three of the six pairs are identical, but the pair 1957 production–1958 survival ranked quite differently. Nevertheless, the hypothesis of an association between level of production and subsequent adult survival may deserve further attention.

CHAPTER 39

FOOD HABITS AND FEEDING BEHAVIOR

DIET AFTER PERIOD OF DEPENDENCE

Methods.—Information from the breeding range is derived from unpublished results of examination of stomach contents and from field observations; food habits in the winter range are known only from published reports. Sources of stomach-content data were 222 stomachs given to me by the U.S. Fish and Wildlife Service, 3 collected by Russell E. Mumford, and 25 analyzed by U.S. Fish Wildlife Service biologists whose records were shown to me by Chandler S. Robbins. Stomachs of specimens collected at unrecorded dates were ignored. Data for *discolor* and *paludicola* are presented separately. All specimens were assumed to be *discolor* except those collected at locations where *paludicola* breeds; many of the latter were labelled as collected in mangroves and were almost surely *paludicola* (see Chapter 1).

Dates of death fell between 1885 and 1950, most of them before 1920. Birds were collected in 18 states, the District of Columbia, and Ontario. No location-specific differences in food habits were detected. Many stomachs were attributed to sex and/or age class by their collectors, but analysis suggested no sex difference in diet (see also p. 488) and no age difference (the sample contained no stomachs of nestlings; see Chapter 24). Therefore data for all locations and sex-age classes have been pooled.

Stomachs supplied by the Fish and Wildlife Service had been stored dry and were soaked in 70% alcohol before analysis. The mean volume of 10 full stomachs was 0.34 ml (SD 0.06 ml); extremes were 0.43 and 0.24 ml. Both the volumetric percentages of the various items in each stomach and the numbers of stomachs in which those items were represented were recorded (see McAtee 1912, Martin 1949, Nolan and Wooldridge 1962). Volumes were measured by displacing water. Many arthropod parts could not be determined below the level of order, and in most stomachs a quantity of finely ground matter, apparently animal, was unidentifiable. All operations referred to in this paragraph were performed by David P. Wooldridge. Terminology for insects follows Borror and DeLong (1971).

Material collected in the breeding range was assorted by month. Tables 175 and 176 show number of stomachs per month in which each order of prey was represented, as well as monthly volumetric percentage contributed by each order to the total food, both determined and undetermined. Each order's monthly volumetric total was obtained by summing percentages for individual stomachs and dividing by the number of stomachs collected that month. Families identified are indicated in footnotes.

Tables 175 and 176 are summarized in Tables 177 and 178, which present additional material described in the following section.

Differences in digestion rates of various prey items are well known to bias results of stomach-content analysis (see Hartley 1948, Custer and Pitelka

TABLE 175
STOMACH CONTENTS¹ OF 208 SPECIMENS OF *D. d. discolor*² COLLECTED
IN THE BREEDING RANGE, ACCORDING TO MONTH OF COLLECTION

Food	Month of Collection															
	March 2 specimens		April 28 specimens		May 93 specimens		June 26 specimens		July 15 specimens		August 25 specimens		September 17 specimens		2 specimens October	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Plant																
Fiber					1	<1	1	<1								
Seeds													1	3		
Animal																
Gastropoda, order undetermined					1	<1										
Acarina					1	<1										
Araneida			10	7	22	4	5	1	1	<1	7	2	4	4	1	3
Ephemeroptera ³			1	1							1	<1				
Orthoptera ⁴					3	1					1	1				
Mallophaga			1	<1												
Hemiptera ⁵			3	1	3	<1	3	2	2	4	1	<1			1	5
Homoptera ⁶			3	1	13	2	7	4	3	3	4	4	4	2	1	3
Coleoptera ⁷	2	30	20	16	69	28	19	28	13	36	20	24	12	14	2	50
Neuroptera ⁸			1	<1												
Lepidoptera ⁹	2	55	11	19	18	10	19	36	5	9	5	10	11	44	1	20
Adult			2	2	3	1	2	2	1	1	1	<1	3	11	1	10
Larvae	2	55	11	18	15	9	17	34	4	8	5	10	8	33	1	10
Diptera ¹⁰	1	10	11	6	34	6	8	4	3	2	10	7	3	2		
Hymenoptera ¹¹			12	15	26	6	8	4	2	1	1	3	5	4		
Eggs, probably arthropod			1	<1	6	1	4	4			3	<1	1	<1		
Undetermined matter, probably animal	1	5	22	33	83	42	20	17	15	45	24	46	15	27	2	20

¹ See text for sources and methods. Percents as rounded do not always equal 100.

² Birds were assigned to race on the basis of place of collection.

³ One family identified: Ephemeridae.

⁴ Two families identified: Acrididae, Tettigoniidae.

⁵ Three families identified: Nabidae, Pentatomidae, Lygaeidae.

⁶ Five families identified: Membracidae, Cicadellidae, Cercopidae, Fulgoridae, Coccidae.

⁷ Ten families identified: Carabidae, Staphylinidae, Elateridae, Buprestidae, Coccinellidae, Tenebrionidae, Cerambycidae, Chrysomelidae, Bruchidae, Curculionidae.

⁸ One family identified: Corydalidae.

⁹ One family identified: Pyralidae (adult). Note that both an overall percentage and separate percentages for adults and larvae are given.

¹⁰ Ten families identified: Culicidae, Bibionidae, Chironomidae, Mycetophilidae, Cecidomyiidae, Asilidae, Empididae, Syrphidae, Sarcophagidae, Tachinidae.

¹¹ Four families identified: Tenthredinidae, Ichneumonidae, Cynipidae, Formicidae.

TABLE 176
STOMACH CONTENTS¹ OF 40 SPECIMENS OF *D. d. paludicola*,² ACCORDING TO MONTH OF COLLECTION

Food	Month of Collection																	
	February 1 specimen		March 3 specimens		April 13 specimens		May 9 specimens		June 0 specimens		July 4 specimens		August 6 specimens		September 2 specimens		October 2 specimens	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Plant fiber					2	< 1	3	1										
Animal																		
Lamellibranchia, order undetermined							1	1										
Acarina							1	< 1			1	1						
Araneida					7	9	5	6			1	1	3	7				
Odonata ³			2	50	2	8	1	3										
Orthoptera ⁴					1	1					2	3						
Psocoptera ⁵					1	< 1												
Hemiptera ⁶					4	2							2	3		1	3	
Homoptera ⁷					4	11	7	13			2	8	2	12				
Coleoptera ⁸	1	10			11	9	6	17			4	40	4	14	2	35	2	13
Lepidoptera ⁹					10	40	4	13					2	14	1	5	1	5
Larvae					9	35	3	11							1	5		
Pupae					2	1							2	14	1	5	1	5
Adult					4	4	1	2										
Diptera ¹⁰			2	18	5	2	3	6			1	1	2	3	1	3		
Hymenoptera ¹¹	1	90			5	5	2	1			1	24	2	3				
Eggs, probably arthropod					3	1	1	1			1	1						
Undetermined matter, probably animal			3	37	5	11	6	33			2	20	5	43	2	55	2	83

¹ See text for sources and methods. Percents as rounded do not always equal 100.

² Birds were assigned to race on the basis of place of collection.

³ Two families identified: Lestidae, Coenagrionidae.

⁴ One family identified: Acarididae.

⁵ One family identified: Liposcelidae.

⁶ One family identified: Hydrometridae.

⁷ Five families identified: Membracidae, Cercopidae, Cicadellidae, Fulgoridae, Coccidae.

⁸ Nine families identified: Malachiidae, Helodidae, Buprestidae, Coccinellidae, Oedemeridae, Anobiidae, Chrysomelidae, Curculionidae, Scolytidae.

⁹ Note that both an overall percentage and separate percentages for adults, pupae, and larvae are given.

¹⁰ Five families identified: Sciaridae, Chironomidae, Syrphidae, Drosophilidae, Calliphoridae.

¹¹ Seven families identified: Eupelmidae, Chalcididae, Cynipidae, Proctotrupidae, Formicidae, Pompilidae, Colletidae.

TABLE 177
ARTHROPOD ORDERS IMPORTANT IN STOMACH CONTENTS OF RACE *discolor*¹
AND RELATIVE SIZES² OF INSECT ORDERS IN NORTH AMERICA

Order	Stomachs in which found		Volumetric % of contents of stomachs		Spp. in insect order as % of all insect spp. ²
	N	%	As a % of identified animal matter	As a % of all matter	
Coleoptera	157	76	42	26	32.3
Lepidoptera	72	35	29	18	12.4
Diptera	70	34	8	5	18.2
Hymenoptera	54	30	8	5	18.4
Araneida	50	24	3	2	—
Homoptera	35	17	4	3	7.3
Hemiptera	13	6	1	1	5.1

¹ See Table 175. Identified animal matter belonging to other orders amounted to 2%.

² Size is in terms of number of species in each order as a percentage of all described insect species in North America north of Mexico. Calculations are based on Borror and DeLong (1971: 89).

1975). No attempt was made to correct for this bias, and the following discussion of contents necessarily proceeds as if they accurately reflected the Prairie Warbler's diet. That certain inaccuracies are in fact present is suggested by (1) the quantity of matter that could not be identified and (2) the absence of a few items, e.g. aphids (see also pp. 26, 487), that I have often seen Prairie Warblers eat.

Results.—Breeding range of *D. d. discolor*: All but a trace (0.3%) of identifiable food was animal, consisting of arthropods and fragments of one snail shell (Table 175). Spiders and representatives of only 6 orders of insects made up over 97% of arthropods. That these same 6 orders are the most abundant in the Prairie Warbler's range is suggested by Table 177, which shows that among all insect species described from North America 94% are from these orders (calculated from data in Borror and DeLong 1971: 89). Great species diversity does not necessarily mean abundance of individuals, but 94% is so high a figure that the great relative abundance of insects belonging to these orders can probably be assumed. If so, the indication is that the Prairie Warbler is a generalist in its food habits, taking whatever is available (see below).

Beetles appear to be eaten in rough proportion to their relative numbers among all insects; chrysomelids and curculionids, which are often small and are herbaceous and diurnal (as far as I can discover; see Lutz 1935: 361), are eaten especially frequently. For example, 17 of 69 stomachs from May contained chrysomelids and 23 contained curculionids. Caterpillars may be taken out of proportion to their numbers, perhaps because of lack of much mobility. But it also seems likely that caterpillars are a more efficient energy source than insects with extensive hard structures such as elytra; the prominence of caterpillars in the diet of nestlings (see p. 269) suggests that they are an efficient food.

Other points concerning the stomachs: (1) The carydalid (Neuroptera) in one was a hellgrammite, presumably taken from a stream (see p. 496). (2) Insect eggs, when they occurred, usually did so in large numbers (to 250); in the field I often saw warblers eat clustered arthropod eggs, apparently taking them one by one. (3) Two stomachs held small pieces of leaf and one held

seven seeds of a berry (*Rubus* sp.). Seeds have been found in Prairie Warbler stomachs collected in Cuba, and a male taken in New York in June (Smith. Inst. N235805) is labelled "stomach filled with insects and seeds." (4) The only seasonal trend evident is the declining volumetric percentages of Araneida and Hymenoptera from April through July and their rise again in August and September. When I swept vegetation for arthropods on the study area at the time Prairie Warblers returned in spring (Chapter 4) spiders were among the few arthropods caught in numbers; and relative to other insects, hymenopterans appeared to be more abundant in spring than in summer.

Families not included in Table 175 but that I saw eaten are tree crickets (Gryllidae:Orthoptera), Psyllidae (Homoptera, see p. 26), Aphididae (Homoptera), Chrysopidae (Neuroptera), and lepidopterans of the families Hesperidae (adults), Sphingidae (larvae), Phalaenidae (larvae and adults), Lasiocampidae (larvae), and Geometridae (larvae and adults).

Other field observations: (1) A male warbler once brought a large millipede (Diplopoda) to nestlings. (2) A female in early May drank sap from a wound on the side of a Black Locust (compare Mousley 1917, Bicknell 1917, Leopold 1924, Kilham 1953, Mayfield 1960: 68-69).

Winter range of *D. d. discolor*: Wetmore (1916: 102) found the following volumetric percentages (rounded by me, nomenclature conformed to Borror and DeLong 1971) in 15 stomachs collected in Puerto Rico: Hemiptera, 1%; Homoptera (all Fulgoridae), 43%; Coleoptera (Chrysomelidae, Curculionidae, Cerambycidae, Elateridae, Dermestidae or Trogidae), 16%; Lepidoptera, 13%; Diptera, less than 1%; Hymenoptera (almost entirely Formicidae), 4%. Spiders contributed 20%; the miscellaneous remainder, less than 4%, was animal.

Danforth (1925: 121) reported that 98% of the food of two males from Cartagena Lagoon, Puerto Rico, was animal, 2% white pithy vegetable matter. The animal material consisted of one fulgorid (Homoptera), two deerflies (*Chrysops vittatus*, Diptera: Tabanidae), one pentatomid (Hemiptera), one small moth, and some beetle fragments (these latter forming 45% of the contents). In a later paper (1931: 94) he stated that the stomachs of two Puerto Rican specimens were filled with insects, very largely elaterid beetles. Bowdish (1903a) reported that stomachs of most Prairie Warblers in Puerto Rico contained insects only, but he found seeds in some Cuban specimens (1903b).

In the Virgin Islands, Danforth (1930: 129) found only insects in three stomachs. Beetles (including Coccinellidae) predominated.

Comparing food of *discolor* in the breeding and winter ranges, the diet seems not to change greatly during the year, although the prominence of fulgorids in Wetmore's sample and the possibly reduced importance of Coleoptera and Lepidoptera in winter should be noted. The conclusion that food habits differ little in the breeding and winter ranges is consistent with inferences about the diets of other parulids, inferred from their foraging behavior (Morse 1971: 189).

D. d. paludicola: The Florida race eats small beetles, especially chrysomelids and curculionids, probably about as often as does *discolor*, although the volumetric contribution of Coleoptera to the Florida sample was lower (compare Tables 177 and 178). Lepidopterans, principally caterpillars, were most important in volume, but the number of stomachs containing these was no greater than the

TABLE 178
ARTHROPOD ORDERS IMPORTANT IN STOMACH CONTENTS OF RACE
*paludicola*¹

Order	Stomachs in which found		Volumetric % of contents of stomachs	
	N	%	As a % of identified animal matter	As a % of all matter
Coleoptera	30	75	22	15
Araneida	16	40	8	6
Homoptera	15	38	14	9
Lepidoptera	15	38	29	20
Diptera	14	35	6	4
Hymenoptera	11	28	4	3
Hemiptera	9	23	3	2
Odonata	5	13	11	7

¹ See Table 176.

numbers in which Homoptera and Diptera occurred. The large number of spiders is a notable feature, as is the presence of aquatic forms (damselflies, a water strider, a bivalve). Several stomachs contained small amounts of plant fiber and one held a few small glassy pebbles or grains of sand.

Indices of food diversity.—Modern foraging studies (e.g. Morse 1970: 142–143, Willson 1970: 170) often employ a diversity index to quantify a species' tendency to specialize or generalize among feeding stations. I have used such an index for food items (not foraging stations) in order to compare the diets of the two Prairie Warbler races and of the sexes of *discolor*.

The equation used is

$$H' = \sum_{i=1}^s P_i \cdot \ln P_i$$

where H' represents the diversity in the sample, s the number of categories of food, and P_i the proportion of food found in category i . The 15 categories of food used were Acarina, Araneida, Ephemeroptera, Odonata, Orthoptera, Hemiptera, Homoptera, Neuroptera, Coleoptera, Lepidoptera adults, Lepidoptera larvae, Diptera, Hymenoptera, eggs, and all other matter (including undetermined). A separate H' value was obtained for each stomach that contained any determinable items. Values were normally distributed, and I therefore obtained their means. Comparisons were made of H' values themselves. Also reported is the ratio $J' = H'/H'_{\max}$ where H'_{\max} represents the situation in which proportions in all categories are equal; values of J' were calculated for means of H' . The smaller the value of J' , the lower the diversity in stomach contents.

The mean of H' for 187 stomachs of *discolor* is 1.220 (SD 0.601) and for 40 stomachs of *paludicola*, 1.288 (SD 0.683). The means do not differ ($P > 0.5$). J' for the mean of *discolor* is 0.312 and for the mean of *paludicola*, 0.330.

The mean of H' for 77 males of *discolor* is 1.230 (SD 0.549) and for 34 females, 1.274 (SD 0.499). The means do not differ ($P > 0.5$). J' for the male mean is 0.315 and for the female mean, 0.326.

DIET OF DEPENDENT YOUNG

What is known about food of young is described in Chapters 24 and 28.

ADULT FEEDING BEHAVIOR

On the study area feeding locations of both sexes ranged from the bare ground to the tallest treetops. Prairie Warblers took items from most or all species of seed-bearing plants as well as from midair. They interrupted virtually every kind of activity to seize food that was spied; thus it is a fair guess that the hellgrammite (p. 486) was seized opportunistically by a warbler that saw it while bathing or drinking. On the basis of the species' tendency to take food during whatever other activity the individual was engaged in, I shall make the assumption (p. 492) that the heights at which individuals were seen imply the heights at which they fed.

Foraging methods.—Gleaning while perched: This description of modes of feeding begins with the most frequent and proceeds in descending order of frequency. The commonest method at all seasons was gleaning while perched on (or hopping along) a diagonal branch or twig with the body approximately parallel to the ground.

Flycatching: The most usual form of flycatching consisted of a level flight out from a perch of any height; the flier suddenly set its wings and slowed almost to a stop while seizing an insect, then either turned and flew back to the original perch or continued to a new perch without turning (compare Griscom and Sprunt 1957: 183; Walkinshaw 1959). Some flights covered 20 m, but most were shorter; the longest were those from higher perches. At times flight angled upward at about 30°; after a pause to seize the insect, the bird glided downward to a new perch. Sometimes a warbler startled an insect into flight, pursued it skillfully (e.g. straight upward or downward), and usually caught it.

Flycatching was much more frequent shortly (1–10 days) after Prairie Warblers returned in spring than it was thereafter. At that season insects appeared uncommon (Chapter 4), and leafless branches and dead herbaceous plants probably offered fewer rewards from gleaning; doubtless it was important to pursue every insect seen, even at the higher energetic cost of flight. An additional cause of the more frequent flycatching in April may have been that the numbers of imagoes were unusually high relative to larvae and other flightless instars.

Males that perched and advertised frequently caught passing insects by flycatching; e.g. one unmated advertising male in May performed flycatching about twice per minute for 1 hour, obtaining all food in this way. Very short flycatching flights (in the herb-forb layer, never involving return to the original perch) were common at dusk, when mosquitoes and gnats were abundant and most other insects probably were less active and less easy to see. Evening flycatching was interspersed with other feeding methods; birds moved rapidly, evidently taking food with great frequency (see below, p. 491); bill-snapping was clearly audible.

Flycatching of another sort was seen once: A female flew into the top of a tulip tree 7 m high, fluttered nearly straight downward through the branches until she reached the ground, then immediately returned to the top of the same tree and repeated this performance (12–15 times). She seemed to seize objects as she fluttered; landing in the tree may have dislodged insects or caused them to fly.

Hovering: Hovering occurred at all heights and was frequently used when taking insects from undersides of leaves (see Walkinshaw 1959) or from flowers or buds of trees; hovering birds picked spiders from their webs. The head and bill were held approximately horizontal; the body hung downward at about 115° from the line of the bill; the feet hung limply downward. Bill-snapping was audible when the prey was seized. Once a male hovered to take a spider from a web, then seemed to fly backward several cm like a hummingbird. Frequency of hovering probably did not vary seasonally.

Clinging to vertical stems: At the beginning of the season birds sometimes clung to tree trunks while picking insects from them. Feeding while grasping the vertical stem of an herb or a forb was common at all times.

Hanging upside down: Hanging upside down in the manner of parids was rather uncommon, although Prairie Warblers appeared adept at it. Sometimes they hung 15–20 sec, occasionally holding on by only one foot, while working persistently to open cocoons or egg cases. The frequency of such feeding probably did not vary seasonally.

Feeding on ground: Flying to the ground to seize a crawling insect was rather common early in spring, rare thereafter. This change in frequency possibly was attributable to greater conspicuousness of ground-dwelling insects before leaves developed, possibly also to seasonal variation in size and age structure of insect populations.

Seizing flying insects while perched: Throughout the season, but never frequently, perching birds grabbed insects that flew by within reach. If the insect was missed the bird sometimes pursued it.

Foraging method and vegetation structure.—The structure of the vegetation in which it was foraging at the moment greatly affected the Prairie Warbler's manner of progressing and capturing food. Because of this fact and because the trees and shrubs of the study area varied greatly in form, it was impossible to categorize the species' foraging using the methods of MacArthur (1958; see also bibliography in Morse 1971).

Examples will illustrate how foraging was affected by vegetation structure: Scrubby White Elms have many branches with numerous twigs and therefore are leafy throughout the entire tree. Warblers fed in all parts of such elms, hopping from twig to twig and usually gleaning while perched. Movement appeared random in direction without any tendency for radial, peripheral, or vertical courses. In contrast, the foliage of redbud and sumac spp. is often concentrated at the top of the tree in a flat or slightly arched canopy. Warblers moved through this canopy and gleaned, or they perched beneath it before flying up to seize food while hovering. Numerous other tree-species-specific examples of foraging method could be cited.

Rates of foraging.—Examples of uninterrupted, normal foraging by birds that were presumably minimally affected by other motivations or constraints, e.g. sexual or agonistic, are reported in this paragraph. The observations were at midday in late summer; food probably was abundant; the individuals were not in molt. (1) A female moved at heights of 0.3–1.3 m in herbs, forbs, and small trees. Her course was erratic and apparently random unless she saw an insect. She changed perch 20–30 times per minute, usually by hops and short flights

(0.1–3.0 m). She bobbed her tail and constantly shifted the long axis of her body as she scanned the surroundings. (2) A foraging female moved about 100 times in 2 min. All but 3 moves were hops and pirouettes (see Ficken 1962b: 153–154) of a few cm, most of them upward in an elm thicket; 3 were flights of about 1 m. All food was obtained by gleaning from leaves and trunks. (3) A male foraged at heights of 1–3 m in a Honey Locust, making a series of 2–3 hops (sometimes half-hop, half-flight) in quick succession along a branch, then pausing slightly before hopping again; motion was nearly constant. All food was seized by hovering under leaves that hung down from branches above the branch along which the bird moved.

Incubating and brooding females when away from the nest foraged at perhaps twice the pace indicated above, presumably because of the limited time available; compare Morse's (1968: 782–783) data for other parulids and his suggestion that for females the period of incubation may be "the most critical one during the breeding season." The impression of very energetic, fast movement was intensified by the greater frequency of flycatching, hovering, and flight from plant to plant. Sometimes females building nests foraged in this way between building trips.

As already indicated, rapid foraging was characteristic before darkness (for about 30 min); foragers seldom moved higher than 1–2 m. The rate of seizing prey and the distances covered by flight were probably about twice as great as during normal-paced foraging. This behavior may have been attributable to the need to increase food intake before fasting and also to the presence of flying insects at dusk. Some dawn feeding was very similar, but in males the tendency to sing at dawn usually dominated all other behavior.

Rapid foraging also characterized the few hours following an individual's arrival from migration (see Chapter 6) and the period of dependence of full-grown fledglings. Parents often darted to an offspring and delivered an item, started to move away but spied an insect, flew instantly to seize it, then dashed back to the young bird. To illustrate, a female feeding young made 4 or 5 deliveries of food per minute for several minutes; a few days later after the fledglings were independent she foraged steadily but leisurely for herself, catching about 2.5 insects per minute.

Short-term tendency to specialize.—Prairie Warblers frequently concentrated on a single prey species for some minutes; examples are psyllids on pines and sumacs (see p. 26), chrysomelid larvae on sumacs, caterpillars common on goldenrod, or spittle insects on a variety of plants (see Nolan 1956). Somewhat similarly, individuals at times confined foraging to particular tree species, e.g. flying from one plum or Sassafras that was in flower to another. This behavior was more frequent early in the season; if food was scarce and/or unevenly distributed, random searching might be expected to be replaced by specialization on plants discovered to be good food sources.

Preparation of food for eating.—Most small arthropods such as spiders, flies, and caterpillars 10–15 mm long were swallowed whole without preliminary treatment. They appeared to be seized in any way convenient. Larger caterpillars (up to about 40 mm long) were nearly always seized just behind the head, then hammered one or more times on a branch. Other large items, e.g. moths,

were also hammered occasionally. The warbler aligned its body almost parallel to its perch (always or almost always facing downward if the branch was not horizontal), raised its head and foreparts slightly, then brought these rapidly downward so that the free-swinging end of the insect snapped against the hard surface (compare Mayfield 1960: 68, Ficken 1962b). The force of the blow was increased by the whip-cracking effect of holding the insect at one end. When blackberry canes were used as the perch, thorns tore the caterpillar's body as the bird pulled its head back from the downward snap. One warbler swallowed a caterpillar after hammering it on a blackberry thorn, then carefully ate insect matter adhering to the thorn. When preparing food for young, some items were softened by holding them crosswise in the bill and passing them back and forth between the mandibles while squeezing.

Large winged insects such as moths 25–30 mm long and robber flies (Asilidae) were sometimes carried to the ground after capture, probably partly because they were often caught near the ground in flight. The insects evidently were immediately hammered against the ground and disabled: when I was able to frighten warblers into abandoning them I found the insects dead or unconscious, their wings and some legs (and once a robber fly's head) removed. I never saw a Prairie Warbler hold food with its feet, and I assume that prey appendages were broken off by grasping them with the bill and hammering the body on the ground (compare Ficken 1962b).

Foraging heights according to stage of reproduction and sex.—Heights at which males perched and foraged varied according to stage of the breeding cycle; heights of foraging by females did not. Note (p. 489) that an individual observed at any height is assumed to have fed most recently, or next, at that height; many observations support the general truth of the assumption.

During the first several hours after arriving on territory from migration males tended to forage at or below 2 m and sought higher elevations only when they advertised and patrolled (Chapter 6). Later, but while still unmated, they ascended to greater heights; among 132 records of heights of advertising unmated males in April (4-year period), the median is 4.7 m. Elevations after pairing were affected by interactions with the female, but males continued to spend much time at high stations until breeding ended. Of 129 heights of paired males in June (4-year period, males at all stages of the breeding cycle), the median was 6.1 m; the data do not differ significantly from those prior to pair formation, above (median test, $P > 0.25$).

Heights of females while gathering nest material, while on or at the nest, or while in the immediate vicinity of fledglings are omitted from the following analysis; to include them would bias the results toward very low heights and assure a difference between males and females. The median of 98 June observations is 1.6 m. In a median test of these and the June data for males, the common median is 3.3 m and the difference between the sexes is manifestly great ($P < 0.001$).

Between the end of reproduction and disappearance of Prairie Warblers in fall the median height of 480 observations of adult males was 1.8 m and of 296 observations of adult females, 1.6 m. Both subsamples include approximately equal proportions of molting and nonmolting individuals. The female median is the same as that for June; the significance of the reduction in the male

median (from 6.1 m in June) is obvious. In a median test of the postreproductive heights of the two sex classes (common median 1.7 m) adj. Chi-square = 6.5; $df = 1$; $P \approx 0.01$. The fact that adult male heights were greater than adult female heights at this time might be accounted for by the renewal of a tendency toward territorial behavior in males that had molted (pp. 436–437). However, this explanation seems doubtful when heights of immatures are examined; 75 records of males and 56 of females have the same median, 2.0 m. Female age classes differed ($P < 0.05$); male age classes did not. I can suggest no explanation, but point out that samples for immatures were small.

The facts (1) that males tended to stay low both immediately after arriving and after breeding and (2) that females did so at all times argue against the possibility that the seasonal variation in height of males was attributable to changes in height of food. Rather, all indications are that optimal foraging heights were always within about 2 m of the ground. Plant biomass at 0–2 m was undoubtedly much greater than at 2–4 m, and the volume of leafy vegetation decreased at progressively higher levels. Assuming that at all relevant dates arthropod abundance was correlated roughly with plant biomass per unit of height, heights frequented by males during reproduction are probably to be explained by the inclination to advertise from elevated perches (see Chapter 29).

Morse (1968: 779), studying four species of *Dendroica* in Maine spruce forests, noted that the males feed higher, resulting “in a situation where males can forage readily while remaining maximally conspicuous, and females can forage in an area maximally adjacent to their nests.” As he pointed out, this tendency to feed at different heights would not increase available resources unless the sexes eat different food. Neither stomach contents nor size and shape of their bills suggested male and female Prairie Warblers eat different food (see pp. 483, 488, and Table 179, p. 504). For that very reason it may be advantageous that the male feed at greater heights and leave the food supply at lower levels for the female. Given the greater energy demands that reproduction imposes on her and the limited time available to her for feeding during much of the cycle, it must be important that she be able to forage with maximum efficiency. Although the result is probably that the male must expend added energy by foraging where food is less abundant, conservation of resources most accessible to his mate doubtless yields a net gain to him in reproductive success.

Heights of foraging in the winter range.—Except for Eaton’s (1953: 171) statement that in Cuba “Prairie Warblers hunted the tops and central areas of the trees . . .,” indications are that in winter the birds usually frequent the shrub layer (see Chapter 2 and Appendix 3).

THE PRAIRIE WARBLER’S FEEDING STRATEGY

Morse (1971) has outlined various adaptive strategies that might be expected of insectivorous birds, and I shall try to relate the Prairie Warbler’s strategy to his model. Factors that should exert pressure toward both generalism and plasticity (such feeders are “the true opportunists,” Morse 1971: 181–182) are its migratory habit and its type-A territoriality. Its site fidelity, especially in males, should also select for breadth of feeding strategy; within an individual’s

lifetime the vegetation on its preferred breeding location can change considerably, bringing in new species of arthropods and calling for new modes of foraging. Indirect evidence that the Prairie Warbler's strategy is indeed plastic and generalized is its wide range of environments inhabited (Chapter 1), arrival on the breeding range when food is probably scarce (Chapter 4), variety of foraging behaviors, and absence of any considerable morphological variation. Its diet points to the same conclusion. The foraging Prairie Warbler probably eats nearly every small insect that it sees, relative importance of insect groups in the diet being largely determined by their relative availability.

Finally, on my study area at all times of the breeding season the warbler's foraging grounds seemed more diversified than those of any other species present. In addition to its characteristic foraging beat in open shrub growth, it entered dense thickets inhabited by skulking insectivores (e.g. White-eyed Vireo), shared margins of woods with forest birds (e.g. wood pewees), and frequented treeless, sunny forb-grass plots with open-field fringillids (e.g. Field Sparrow).

CHAPTER 40

MAINTENANCE BEHAVIOR OTHER THAN FEEDING; MISCELLANEOUS BEHAVIOR

MAINTENANCE AND COMFORT ACTIVITIES

Preening.—Birds preened at all times of day throughout the breeding season, often in association with other comfort movements; preening was frequent in the early morning, especially when there was dew. Molting birds sometimes preened for 30 min almost without interruption.

The bill at times touched the uropygial gland, probably most frequently before preening the primaries. The body, wings, and/or tail were moved (“contorted” according to Simmons 1964) into position to allow the bill to reach the region to be preened; the head and neck extended toward this objective. A feather (perhaps sometimes several feathers) was grasped at its base and the bill thrust from the feather’s proximal toward its distal end, causing the rachis to pass between the slightly opened mandibles. Sometimes the bird appeared to raise its head a little during this thrust, which might lift the feather and increase friction between it and the bill. The movement usually was quick; no “nibbling” was noticed (see Ficken 1962b, Simmons 1964).

Each of three positions of the wing permitted preening of a different group of feathers. (1) To preen the remiges, alula, ventral wing coverts, and the anterior part of the body near the shoulder, the bird brought the humerus forward and raised the elbow somewhat, extended the forearm to open the wing slightly, and extended the wrist enough to separate the primaries from contact with the secondaries. This movement caused the wing to be cupped or hollowed with its ventral (concave) surface facing somewhat forward, the primaries hanging perpendicularly. The bird could now twist its head and neck to one side, take the base of a feather between its mandibles, and thrust its head outward; the full length of the rachis passed between the mandibles. (2) To preen the region of the body normally covered by the distal portion of the folded primaries, possibly also to preen the feathers of the proximal part of the wing toward the trailing edge of the dorsal surface, the humerus was brought far forward and the wing opened outward somewhat. The actor now twisted its head and neck back over its humerus and preened the exposed flank and possibly the proximal part of the wing. (3) To preen the dorsal wing coverts, the wing was extended outward to about one-third its length and dropped.

To preen the ventral tract, the bird thrust its head straight downward and backward, sometimes leaning far over and preening between its legs (possibly as far as the base of the tail). If the point to be preened was the throat or upper breast, the body was erected, the neck stretched upward, the head pulled back and then turned sharply downward to permit contact of the bill with the body.

To preen the base of the tail (dorsal and lateral surfaces), the tail was bent sharply to one side and the head turned back over the shoulder, the bill pointing at the objective.

To preen the back, the head was turned over the shoulder and the neck was extended. The bill was thrust among the back feathers, the head then raised and simultaneously pushed farther backward toward the tail, evidently passing the preened feather(s) between the mandibles from base to tip.

Bathing.—Bathing in streams or in standing water was rare. In four of five observed cases, the bather was not visible clearly enough to reveal details. In these four, bathing was in streams 2–5 cm deep. One female dropped nest material to bathe. A male hopped back and forth on a branch 0.3 m above the water, looking down as though reluctant, then jumped in and remained for 2 min.

In the case in which details were observable, a female flew to crouch 5 sec in a pool 30 cm in diameter and 2.5 cm deep. While crouching, she flicked her wings rapidly and splashed water on herself. She then hopped out and preened and dried herself for 3 min, returned to the pool for 5 sec and crouched, raised and opened her bill while moving her mandibles, then left the water. This apparent drinking suggests the female had lowered her head into the water (see Simmons 1964). Compare Mayfield (1960: 67), Ficken (1962b), Slessers (1970).

In all months Prairie Warblers bathed in dew and raindrops on leaves; the onset of rain sometimes instantly stimulated bathing. The behavior appeared not to be highly stereotyped: At times birds flicked wings and tail (as in drying movements, below) to shake leaves; at other times they simply leaned forward or sideward, or extended or ducked the head, and rubbed against wet surfaces. Some went from cluster to cluster of leaves, bumping into these and dislodging water. Bathing sometimes lasted 5 min. A case demonstrating the variability of leaf-bathing occurred when I was watching two adult males, one of them molting, on a very hot, mid-August afternoon. A light rain began and both immediately bathed, using the following movements: They flew at and collided with clusters of leaves, shaking water on themselves; while perched next to or under leaves, they fluttered the wings and moved the tail vigorously from side to side for 1–2 sec, with body feathers puffed out; they perched motionlessly on bare branches as though exposing themselves to the falling rain. This bathing lasted 4–5 min, although the rain stopped after 3 min; preening followed. Compare Haverschmidt (1953), Mayfield (1960: 67), Ficken (1962b).

Drying.—Sometimes warblers simply ruffled their wet body feathers and shook themselves vigorously. However, wing-shuffling (Ficken 1962b) accompanied by tail-fanning or, more usually, tail-shaking was a more frequent form of drying. In this behavior the head and neck appeared to be almost motionless, while the wings fluttered very rapidly at the sides and the tail either fanned quickly in and out or jerked from side to side; sometimes the body leaned forward slightly, the region of the tail raised a little. Drying movements lasting 1–2 sec occurred in bursts about 10 sec apart; intervals between bursts were often devoted to preening, sometimes to stretching. At times only the wings moved, barely perceptibly; and tail movements probably occasionally occurred in the absence of wing-shuffling. Drying and preening often lasted 2–3 min (maximum 6–7 min), and almost always followed, or interrupted, bathing. But occasionally the behavior was observed in birds that appeared to have had no recent opportunity to feel or see water (see Ficken, 1962b).

Body-shaking.—Vigorous shaking of the body, usually with the feathers somewhat erected, was often interspersed with drying and sometimes with scratching and preening (compare Ficken 1962b). Occasionally a bird that I released after examining it for molt shook itself vigorously. After defecating, Prairie Warblers jerked the body up and down quickly and vigorously two or three times by a rapid flexing of the legs and tarsi. This behavior perhaps prevented excrement from adhering to the body or plumage.

Head-scratching.—Prairie Warblers scratched the head (chin, cheek, base of bill, throat, crown, occiput) by dropping a wing and extending a foot over it in the indirect method (compare Ficken 1962b). The head was stretched forward or turned at various angles, depending upon the part to be scratched. In about 75% of all cases the scratching bird opened its bill, sometimes widely, usually doing so the moment it began to scratch but occasionally just before scratching; the two behaviors either ended simultaneously or the bill was closed first. Ficken (1962b) states that certain parulids open the bill widely when the head is extended forward and slightly or not at all when the head is down or to one side; Prairie Warblers probably conformed to this pattern. Bill-opening sometimes appeared to be reflexive and associated with sudden onset of scratching; it may occur less often when scratching is part of a series of systematic comfort movements or is prolonged. Preening, stretching, and sunning frequently preceded, followed, or were interspersed with scratching. Often birds alternately and regularly scratched one side of the head, then the other. (Page 499 describes behavior that may have served to scratch the rictal region.)

Stretching.—(1) In the most often seen movement (the side-stretch) the bird stretched one wing outward, backward, and somewhat downward; slowly fanned the ipsilateral half of the tail outward and tautly thrust the ipsilateral leg downward, slightly outward, and backward; the leg was fully extended and touched or nearly touched the outer part of the fanned tail. About halfway through the stretch, the bird also opened and slightly raised the opposite wing. In the most complete stretches the wing on the stretched side appeared to be extended 75–100%, the other wing 25%. After a barely perceptible pause at the end of the stretch, the normal perching position was resumed. The movement lasted 1–2 sec. (2) In the upward-leg-stretch the actor straightened its legs and feet fully, thrust its head and neck upward to maximum height, and from this upright position slowly leaned forward in a bow that it interrupted momentarily when the body was about horizontal; the bow then continued until the back was hunched and the head and sometimes the tail were slightly below horizontal (one male raised its left foot from the perch at this point). Normal perching was then resumed. This stretch lasted about 1 sec. (3) In the upward-wing-stretch the wings were raised simultaneously over the back until the arms (not hands) were nearly parallel to each other. The hands were extended outward; thus the stretched primaries were approximately parallel to the ground. The legs and feet probably were not stretched, but these behaviors were variable, as the next paragraph describes. This stretch too lasted about 1 sec.

Upward-leg- and upward-wing-stretches often followed each other in quick succession; occasionally some elements of one seemed to be incorporated into the

other. At times movements appeared to be rearranged into novel sequences, and new movements may even have been introduced. For example, a male raised his wings, hunched his head forward in a bow, brought his still-open wings down somewhat below horizontal, then closed his wings and resumed the normal perching position. A fledgling 29 days old lowered both wings simultaneously and stretched them while standing in the upright position of the upward-leg-stretch; and an adult male extended its wings slightly downward before the terminal bow of the upward-leg-stretch. Stretching the wings downward is a transitional stage in some parulids (see Nice 1943: 44, Ficken 1962b; see also pp. 298 and 301) but is retained by some adult passerines (Andrew 1956b).

In 9 of 11 sequences consisting of two stretches, the upward-leg-stretch was combined with one of the other types of stretches; it was performed first in 6 of these cases. The side-stretch (which occurred alone more often than the others) was present in eight sequences in combination both with a second side-stretch and with the other kinds of stretches. The upward-wing-stretch was present in four sequences, was first in 1 of them. A few sequences of three stretches were noted.

Sunning.—In the simplest form of sunning, the bird perched quietly in full sun, sometimes preening occasionally. This basking was most frequent on cool mornings shortly after sunrise; sometimes it was seen in molting adults. At a slightly higher intensity, basking and preening were associated with ruffling the feathers, especially those of the back. In the next stage, the wings were drooped, the back feathers conspicuously raised, the tail spread to about 5 cm at its tip, the back turned directly toward the sun. One bird in this position seemed to thrust its head forward; another may have turned the side of the head to the sun. This form of sunning lasted some 30–45 sec; it was sometimes assumed suddenly (once by a 34-day-old young), as though it were a reflexive response to exposure to the sun. One male interrupted sunning to scratch the sides of the head alternately.

If there is a typical intensity in the Prairie Warbler's sunning behavior (see Simmons 1964: 282), it is probably the following form (compare Hauser's (1957) Level III), which I observed many times: A warbler on a sunny perch would suddenly lean to one side, lowering that side; rotate the body on its long axis causing the other side to turn upward to the sun; extend and fan (50–100%) the wing on the upward side of the body; stretch the spread wing backward so that the distal portions of the inner secondaries overlay the feathers of the back; rotate the neck to expose the side of the head and throat to the sun; spread the tail to about 5 cm at its tip and twist it toward the side of the body presented to the sun, tilting it so that its plane was approximately parallel to the ground. The plumage was somewhat ruffled, the bill usually opened, the eye toward the sun possibly closed. The position usually was maintained 30–45 sec and sometimes was repeated after a brief interruption; occasionally it lasted 2 min. The behavior often began without any apparent change in the bird's situation to cause it, but at times it was stimulated by sudden exposure to the sun; at such sudden exposure birds might immediately stop foraging, preening, or gathering nest material and begin to sun themselves. This form of sunning was seen at all hours and dates, when air temperature was at or above about 19°C.

The most intense form of sunning (Hauser's (1957) Level IV) was seen only once; a detailed description has been published (Nolan 1960).

Bill-wiping.—The actor drew its bill backward from base to tip, wiping the commissure along the branch or twig on which it perched. The movement was rapid and was usually (always?) performed in multiples of 2, wiping both sides of the bill alternately. Wiping was common after eating but also occurred during male agonistic encounters, possibly as a displacement activity. Clark (1970) reports that both Yellow and Prairie Warblers wipe the bill during pauses in singing, with no associated condition that might account for displacement activity. A 60-day-old female that I released after examining her plumage flew to a perch, shook herself, and wiped each side of the bill four times; the circumstances suggested grooming the feathers. Occasionally adults and independent immatures pushed the bill forward, wiping it from tip to base. In two cases observed from close at hand, one bird had been foraging, and the other had just emerged from a stream bath and was drying itself and preening. Both these two held the bill wide open; one wiped once on only one side, the other probably alternated sides. This movement is slower than the common form of bill-wiping; it may function to scratch the region just posterior to the bill.

Resting.—Six times Prairie Warblers (two males, four females) rested from 2–19 min. Both observations of males were on the morning they arrived on the study area in April; the episodes were similar, and only one will be described: A male, which had appeared at 0657 and had fought a male Prairie Warbler and a goldfinch at 0718, when 0.6 m high in a pine puffed out his feathers and became still except for occasional slight head movements. He sang five very faint Trills, then hopped to a lower branch and perched motionlessly for 4 min while occasionally singing almost inaudibly; he looked asleep at times. The behavior ended when another male approached him. Two females rested between acts of nest building, for 5 min (at 0630) at a height of 11 m and for 6 min (at 1330) at a height of 0.7 m; their eyes closed occasionally, and slight head motions were the only movements observed. A female on the day before she laid egg 1 perched quietly for 5 min (at 1530) at a height of 0.3 m, her feathers so puffed that she appeared nearly round. Air temperature was 12.8°C. Finally, a female fed on the ground for 5 min after a sexual chase and tail pulling (Chapter 10). At 0715 she flew to a perch 1 m high, sat motionlessly for 6 min, hopped 2–3 cm and sat another 3 min, hopped to a new perch, and became motionless for 10 min. Throughout, her eyes closed occasionally for a few seconds and appeared only half open much of the time; her feathers were much puffed out; the day was windy, the temperature 13°C (compare Ficken 1962b).

Sleeping.—Females dozing on the nest during the day retracted the head slightly and faced forward. Flashlights directed on nests at night always revealed the birds in this position, but at least some had heard my approach and may have moved. Once a 13-day-old fledgling on a branch dozed 30 sec with its neck retracted, head turned, bill on but not under the scapulars. According to Ficken (1962b), in American Redstarts this behavior typically precedes placing the bill among the feathers; see also Mayfield (1960: 68).

Going to roost.—I made persistent efforts to follow Prairie Warblers to roost

and succeeded only four times. Three other times I accidentally flushed warblers that were apparently roosting. All 7 birds roosted at heights between 74 and 150 cm, near the tops of small trees standing among herbs and forbs in open fields. Details of two episodes follow; for the relationship between times of roosting and civil twilight, see Figure 9 (see also Chapter 28 for fledgling behavior). (1) A male foraged rapidly in herbaceous growth, then suddenly at 2019 (4 July) flew to a Sassafras 1 m high, perched among the terminal leaf cluster of the main stem, and remained motionless until darkness made him invisible. His tarsi were flexed and his belly seemed to rest on the perch in the posture often assumed by young fledglings (pp. 301, 314–315). I could not see the position of his head. The tree was at the edge of a dense 4-m-high clump of Sassafras; surrounding herbaceous plants were almost as high as the bird's perch. (2) A female foraged quickly at dusk and at 2037 (22 June), 3 min after the last Prairie Warbler song, flew to a Sassafras 0.8 m high among grasses and sparse herbaceous growth. She instantly became immobile in the terminal leaf cluster of a diagonal branch, at a height of 74 cm. Her abrupt termination of foraging and short flight to the tree suggested that it was a predetermined roost toward which she had been moving. After 7 min I approached to verify her presence; she flew out, then hopped around nearby as though eager to return, like a bird prevented by fear from going to its nest. (A male once behaved similarly after being flushed from a roost.) I left so that she could return, but next day there were no droppings under the tree; 2 days later I watched the tree until nightfall, but no warbler went to it.

Other evidence supports the suggestion that roosts were sometimes selected prior to darkness: Several males that at dusk had been foraging within small areas suddenly stopped and flew considerable distances (e.g. 40 m) to low thickets into which they disappeared. Similarly, a male I was following went to a 1-m-high White Pine and became immobile but left after 15 sec; he returned to the site in 5 min but left after 10–15 sec; possibly I was too close to him. Accumulated droppings were present under the tree next day, but I removed these and no more accumulated. (This episode was in April, when most deciduous trees lacked leafy cover; another April roost was in a Red Cedar.)

Two cases suggest that roosts may sometimes be higher than those reported above. In both I went to nests at dark to see if fledglings had left; adults, probably females, immediately began to call from heights of 3–4 m in clumps of trees some 25 m from the nests. Walkinshaw (1959) believed that a male Prairie Warbler roosted in the dense branches of a White Pine near his nest.

MISCELLANEOUS BEHAVIOR

Crown-raising.—Birds of both sexes occasionally erected and depressed crown feathers when alarmed and also when apparently merely alert or curious (see Andrew 1961: 338–339), e.g. when I held them just after capturing them, when looking at a Screech Owl (see p. 473), and when watching me after being attracted by my hissing. While Ficken and Ficken (1962) associate crown-raising in parulids with possession of distinctive crown markings, Foster (1967b) also reports the behavior in warblers that, like the Prairie Warbler, lack such markings.

Tail-bobbing.—The Prairie Warbler's well-known tail-bobbing has been inadequately described. It consists of a quick downward movement (maximum about 1.5 cm at the tip) followed by a somewhat slower return to the original position. A slight lateral component is also frequent, so that the tip of the tail describes a small arc laterally as it descends. Although this lateral movement sometimes appears to be the result of a small shift in orientation of the entire body during bobbing, at other times it seems to be an independent sideward movement of the tail. Often only one complete bobbing movement is performed; at other times several bobs follow in succession (see below). Even at full amplitude and maximum frequency, the tip of the tail never rises above the point from which the downward movement began; and the line of the tail when it is raised is approximately parallel to the ground.

Both sexes bob the tail, especially in situations causing nervousness or alarm, e.g. during mobbing of predators. Females bob the tail considerably more often during courtship than after pair formation. In this case the behavior may be associated with initial apprehension of the male; but since it causes the female to be more conspicuous to the human observer, it may function to keep her visible to the prospective mate (compare Andrew 1956a: 195–196, Mayfield 1960:65–66).

Allen's communication to Bent (1953: 433) that the Prairie Warbler "has a habit of twitching its tail nervously from side to side" appears to have led Ficken and Ficken (1962) to classify this species' tail movement as different from that of Kirtland's and Palm Warblers. Others (Wing 1933, Mayfield 1960: 65–66) who are familiar with all three species evidently regard their tail movements as much the same, differing only in details such as frequency and amplitude of vertical movement. I believe that the bobbing of the Prairie and Palm Warblers is similar; I have not seen Kirtland's Warbler.

Andrew (1956a: 179) states that tail-bobbing belongs to a group of behaviors "given when a tendency to fly is accompanied by a tendency . . . to give some incompatible response (which may be a tendency to remain still)" and associates bobbing by the Palm Warbler with its ground- and branch-feeding insectivorous foraging habits (*op. cit.*: 190). Mayfield (1960: 66) suggests that this behavior in Kirtland's, Palm, and Prairie Warblers is related to their brushy, semi-open country habitats and that it functions "as a recognition signal of particular value to birds that see one another frequently through narrow, horizontal vistas."

Homing.—A male caught on the day his young left the nest and carried in an opaque paper bag 4.8 km northward was back singing on his territory 24 hours later.

Unusual reactions to humans.—Often (some 25 times) Prairie Warblers flew (zoomed) within 1 m of my head when I was in full view and could easily have been avoided at a safer distance. The behavior suggested the threatening flights that some species (e.g. Screech Owls, American Robins) direct at humans near the nest; twice it was given when I was near a nest and/or fledglings. However, most such flights were very early in the season and were performed by males, usually when engaged in courtship or fights; suddenly the bird would fly silently (no bill-snapping) so close to me that I would duck. Suggesting that some of these flights were threats is the fact that one male probably crouched tensely after zooming past me (see Chapter 7).

Occasionally males appeared to perform moth flight and butterfly flight (see Chapter 7) directed at me.

Rubbing body on limb.—An unmated male while hopping through branches in midseason extended his wings slightly, fluttered them, lowered his cloacal region and appeared to rub it on a branch for 1 sec. The behavior resembled male copulatory movements; it was repeated 3 times in 1 min.

CHAPTER 41

PLUMAGES, MEASUREMENTS, AND MOLTS OF BIRDS PAST THE AGE OF DEPENDENCE

RELIABILITY OF USING PLUMAGE COLOR IN AGING AND SEXING

Aging.—Prairie Warbler young of the year are readily recognizable as such by plumage color (see frontispiece). Thus, when Russell Mumford and I aged Florida autumn tower kills (Chapter 36) by inspection of plumage and checked our results by examining skull ossification, we made no errors on 332 specimens (101 immatures; compare Nolan and Mumford 1965). Despite a partial prenuptial (prealternate) molt by yearlings in spring, all or nearly all young females retain traces of the first nonnuptial plumage and can therefore still be aged during the breeding season; some yearling males can be aged, but many cannot. Plumages characteristic of the various sex and age classes (subsequent to the age of dependence) are described in Appendix 5.

It is critical to many analyses in preceding chapters to establish that few if any yearling females went unrecognized as yearlings. The evidence that I could age this sex follows: (1) All females banded as nestlings and seen the following spring retained some of the plumage by which young are distinguishable in autumn; they lost this in the first postnuptial (prebasic) molt. All unbanded females considered to be yearlings because of plumage also lost that plumage in the postnuptial molt. (2) Wing measurements of breeding females bearing color traces of the plumage of immature birds differed from wing measurements of females not bearing such traces; on the other hand, wing measurements of the group identified as yearlings were the same as measurements of females in their first autumn of life. Details are given on pages 504–505. (3) The percentage of breeding females retaining colors from the first nonnuptial plumage exactly coincided with the percentage of females expected to be yearlings, an expectation based on the adult male annual mortality rate (see Chapter 38). The statements numbered 2 and 3 cannot be made with respect to males.

Sexing.—Mumford and I sexed tower kills by inspection of plumage (see frontispiece), then checked our results by examining gonads. Among 355 adults in autumn and old birds in spring (189 males), we sexed 3 specimens (1%) wrongly. Of 82 immatures in autumn (19 males), we sexed 3 (4%) wrongly and of 44 recognizable yearlings in spring (25 males), 3 (7%) wrongly.

MEASUREMENTS

Mumford and I measured the wing, tail, tarsus, and bill of most autumn tower kills; these showed very little feather wear. The chord of the culmen was measured from the base of the bill; other measurements were made as shown in Palmer (1962: 5); see also the footnotes to Table 179. We traced outlines of wings of many specimens and from these obtained approximate wing areas according to wing length; data are reported in Nolan and Mumford (1965: 326–

TABLE 179
SELECTED MEASUREMENTS, ACCORDING TO SEX AND AGE¹

Measurements ²	Male		Female	
	Adult	Immature	Adult	Immature
Wing length ²				
N	156	32	117	74
Mean	57.3	55.8	54.2	53.1
SD	1.4	1.2	1.5	1.4
Extremes	61-53	58-54	58-51	57-51
Tail length ²				
N	151	31	117	73
Mean	47.3	47.1	45.6	45.8
SD	1.7	1.6	1.7	1.6
Extremes	54-43	50-44	49-41	50-40
Tarsus length ²				
N	155	31	116	73
Mean	18.71	18.89	18.27	18.52
SD	0.75	0.78	0.78	0.79
Extremes	20.8-17.0	21.7-17.6	20.0-16.2	20.2-17.1
Bill length ²				
N	104	25	78	43
Mean	13.77	13.78	13.48	13.41
SD	0.53	0.62	0.67	0.56
Extremes	15.2-12.5	15.3-12.0	14.7-11.4	14.7-12.2

¹ Measurements are in mm and were taken from autumn specimens in fresh nonnuptial plumage; see pages 503-504. Birds were sexed by examination of the gonads and aged by examination of the skull.

² See pages 503-504 for methods.

327) and not repeated here. I also measured flattened wings of many museum specimens, none believed to be *paludicola* (see p. 360 for the institutions). Some obviously had been wrongly sexed and/or aged; I relied on my own judgment except in cases in which labels gave gonad or skull data. Wing lengths of immature male and female classes netted on Island Beach, New Jersey, are also given.

Migrants through Florida.—Table 179 presents measurements of sex-age classes. Statistical tests reveal the following: Adult wings were significantly longer than wings of immatures of the same sex, and males had significantly longer wings than females of the same age ($P < 0.001$ in every case). Tail length differed between the sexes ($P < 0.001$) but not between age classes of the same sex. The tarsus of the adult male was longer than that of the adult female ($P < 0.001$), that of the immature male longer than that of the immature female ($P < 0.05$). The immature female tarsus was longer than that of the mature female ($P < 0.05$). Bill length differed only as between the sexes (adult males vs. adult females, $P \approx 0.005$; immature males vs. immature females, $P < 0.025$).

Museum specimens.—Wing lengths of birds collected from August through December in the winter range did not differ from those of tower-killed migrants of the corresponding sex-age class. Mean measurements in mm follow: for 28 adult males, 57.4 (SD 1.5); 69 immature males, 55.6 (SD 1.4); 16 adult females, 53.7 (SD 1.5); 56 immature females, 52.6 (SD 1.4). For comparison, measurements of wings of museum specimens collected in continental United States in the breeding season (1 April to start of postnuptial molt) follow:

115 old males, 56.4 (SD 1.4); 32 yearling males, 55.2 (SD 1.4); old females, 53.4 (SD 1.4); 23 yearling females, 52.0 (SD 1.0).

To return to plumage color as a reliable indicator of age, it will be seen that mean wing length of each sex class of Florida autumn immatures was about the same as the mean of museum autumn immatures of that sex and also the mean of museum yearlings collected during the breeding season. (Wing lengths of breeding-season yearlings were slightly shorter, probably because of greater abrasion.) Wing lengths of museum autumn adult females and museum breeding-season old females are the same. If any large number of yearlings, with their shorter wings, had gone unrecognized and been included among breeding-season old females, mean wing length of the latter sample would be expected to be shorter than that of autumn adults. Such a failure to detect yearlings probably explains why museum autumn adult males have significantly longer wings ($P < 0.001$) than breeding-season old males; the mean of the latter group is doubtless reduced by inclusion of many unrecognized yearlings.

Migrants from New Jersey.—Mean wing length of 26 immature males netted in fall at Island Beach, New Jersey, was 56.1 (SD 1.8 mm). The mean for 26 immature females was 53.2 mm (SD 1.5 mm). These data were supplied by Bertram G. Murray, Jr., Joseph R. Jehl, Jr., and James Baird.

PTERYLOSIS

Appendix 6 describes the pterylosis of the Prairie Warbler.

PRENUPTIAL MOLT

This analysis is based principally on museum specimens killed between 1 November and 1 May. Some museum specimens collected in the winter range in November were in late postnuptial or early prenuptial molt. They were just beginning to renew feathers on the head and neck, to which the prenuptial molt is usually limited. I therefore classed this as prenuptial molt.

Terms to describe age classes are "young" for birds in the first winter and spring of life, "old" for all others.

Timing.—Earliest dates of collection of molting specimens were as follows: old males, 1 November; young males, 1 November; old females, 8 November; young females, 16 November. The latest dates, based on spring tower kills, were for old males, 11 April; for young males, 3 May; for old females, 27 April; for young females, 18 April.

Table 180 shows numbers and percentages of winter-range museum specimens in molt between November and April. Pooling data for the sexes, the monthly percentage was 13% in November, then increased gradually until an abrupt rise to 62% in February, declined slightly in March, and dropped to 21% in April. These highly variable results suggest that most birds probably start to molt 3–4 weeks before beginning spring migration (Chapter 3). On many tower kills the process was not yet complete (Table 181). Usually molting tower kills had only a few partly sheathed feathers on the head and/or neck; but a male killed 11 April was molting heavily on the coronal, auricular, inter-

TABLE 180
FREQUENCY OF OCCURRENCE OF PRENUPTIAL MOLT ON MUSEUM SPECIMENS,
ACCORDING TO MONTH AND SEX

Month	Males			Females		
	N	Molting		N	Molting	
		N	%		N	%
November ¹	32	4	13	15	2	13
December	26	6	23	26	3	12
January	37	13	35	18	3	17
February	38	27	71	23	11	48
March	69	44	64	58	20	35
April	15	1	7	19	6	32
Totals	217	95	44	159	45	28

¹ See page 505. All specimens were collected in the winter range.

ramal, and submalar regions, as well as lightly on the abdominal region. Occasional migrants had heavy molt on the crown, the throat, or both.

Date of molt probably did not vary according to sex, although extent did so. Graphs of monthly percentages of molting museum males and females produce curves (not shown) whose shapes are almost identical until April. In that month the proportion of molting males dropped sharply, whereas a substantial proportion of female museum specimens was still in molt. While this suggests (on the basis of 34 specimens) that some females molted after males, evidence from tower kills suggests the opposite (Table 181): 13 of 71 males (18%) were molting in the period 1–20 April, as opposed to only 3 of 31 females (10%).

The only information bearing on duration of the individual's molt is the monthly percentages. The sharp increase between January and February, the

TABLE 181
FREQUENCY OF PRENUPTIAL MOLT ON MIGRANTS THROUGH LEON COUNTY,
FLORIDA, ACCORDING TO DATE, SEX, AND AGE

Dates	Class ¹			
	Old males	Yearling males	Old females	Yearling females
March				
N molting	3/22	1/1	0/4	0/1
%	14	100	0	0
1–10 April				
N molting	10/33	0/1	2/7	0/2
%	30	0	29	0
11–20 April				
N molting	2/26	1/11	0/18	1/4
%	8	9	0	25
21–30 April				
N molting	0/7	0/2	1/30	0/14
%	0	0	3	0
May				
N molting	0/1	1/1	0	0/2
%	0	100	—	0

¹ Some yearling males were surely unrecognizable as such and were entered in the table as old males.

high February percentage, and the large decline between March and April suggest a maximum duration of about 60 days. As will be seen below, both extent and degree of synchrony of the individual's molt probably varied, which would affect duration.

Extent.—Except for a tower-killed male with sheathed abdominal feathers, molting tower kills were renewing feathers on approximately the anterior half of the head and neck.

Numbers of new feathers varied greatly. On some birds killed in April and May and examined microscopically, all feathers on the regions that molt appeared new. Other specimens appeared to have no new feathers, and many had both old and new. This variation was associated with sex, with males molting more heavily. I classed museum skins as in heavy molt if most of the anterior half of the head was affected, with numerous sheathed feathers on more than one region. In heavy molt were 33 (16%) of 210 males but only 6 (4%) of 159 females (adj. Chi-square = 12.4; $df = 1$; $P < 0.001$). Further, among specimens showing no molt at all females outnumbered males; Table 180 shows that in every month but two the percentage of molting males exceeded that of females. Theoretically, this difference could be overcome if females molt later and many more females than males molt in April. However, the evidence from the tower kills (Table 181) suggests no such schedule difference between the sexes, as already stated. The fact that more yearling females than males can be aged by plumage is consistent with the evidence that females molt less heavily than males and that more of them may not molt at all (compare Foster 1967b: 182, 186; see also Hamilton 1961, Hamilton and Barth 1962).

Regions on which museum specimens were molting and frequencies by sex and age are shown in Table 182. The interramal, submalar, malar, and frontal regions were affected most often; but the uneven distribution of dates and the individual variation in timing make conclusions from this evidence tentative. The sexes seem about the same with respect to the regions that molt, except that males may have a greater tendency to replace auriculars (Table 182).

Numbers of birds in molt did not differ according to age class within each sex. Considering only specimens that were molting, in neither sex did extent of molt vary with age (compare Dickey and van Rossem 1938: 499; Foster 1967b: 186–190).

Largely because of the variation in extent of molt, I gathered little information about the order in which regions became involved. On some specimens all feathers appeared to be at the same stage of growth on several regions. However, frequency distributions according to region of the body and month of collection reveal differences at various dates, which may be attributable to the existence of a sequence in some individuals. Only data for males will be used to demonstrate this: Eight of 13 molting museum specimens from January were in molt on the frontal and/or coronal regions; those regions were molting on only 3 of 19 males from March; adj. Chi-square = 5.3; $df = 1$; $P < 0.05$. Among the January males were 5 molting on the interramal and 3 on the submalar region; the March males included 13 molting on the submalar region and 8 on the interramal region; adj. Chi-square for the submalar region = 4.7; $df = 1$; $P < 0.05$. It therefore appears that forehead and crown tend to finish molt

TABLE 182
FEATHER TRACTS AND REGIONS IN PRENUPTIAL MOLT¹ ON MUSEUM
SPECIMENS COLLECTED² OUTSIDE THE UNITED STATES

Region	Old males ³ (50 specimens)		Young males ³ (45 specimens)		Old females ³ (18 specimens)		Young females ³ (27 specimens)	
	N	%	N	%	N	%	N	%
Frontal	17	34	11	24	1	6	9	33
Coronal and superciliary	9	18	10	22	2	11	2	7
Loral	6	12	10	22	2	11	6	22
Ocular	2	4	2	4	2	11	2	7
Auricular	12	24	16	36	4	22	2	7
Malar	20	40	25	56	4	22	11	41
Interarmal	25	50	19	42	4	22	10	37
Submalar	19	38	25	56	9	50	7	26

¹ Many specimens were not molting; see Table 180.

² Dates of collection ranged from November through early April and were not evenly distributed over this period, but calendar distribution was about the same for every sex-age class.

³ See definitions, page 505. Some yearling males were doubtless unrecognizable as such and were entered in the table as old males.

before chin and throat, and that molt persists longest on the throat. The condition of tower kills supported this conclusion.

POSTNUPTIAL MOLT: SEQUENCE

Methods.—Eleven living or freshly killed specimens from Bloomington were closely examined and will be referred to as "molting specimens." Museum skins, tower kills, and birds examined less exhaustively in the field contributed additional information.

When two feathers of the same region and of about equal size (at full growth) were at different stages of development on an individual, I assume that the more developed of the two had begun to grow first. When two locations on the same tract showed a clear difference in proportion of feathers at a given stage of development on an individual, I assume that this reflected a difference in times at which the locations had begun to molt.

Order in which certain tracts began to molt.—Primary 1 was lost at the beginning of molt, probably before molt became discernible on free-living birds (compare Stewart 1952, but see his Table 2; Foster 1967b: 190). As evidence, one molting specimen lacked only primary 1, secondary 8, and possibly a few small body feathers; another specimen had begun to replace primaries 1 and 2 when the only other molt was loss of a few feathers from the frontal, posterior occipital, and sternal regions.

Molt was usually first detectable in the field on the dorsal, or sternal and axillary, or (less often) occipital regions (compare Mayfield 1960: 139–140). Shortly afterward or perhaps concurrently, the upper and undertail coverts were dropped; at about the same time the humeral and femoral tracts began to molt. The next conspicuous change, after the body and head began to become noticeably ragged and patchy looking, was loss of the inner rectrices. By this time several new primaries had begun growth. Loss of secondaries was not observed in the field but must have been about simultaneous with loss of rectrices; Table 184,

TABLE 183
PROBABLE ORDER IN WHICH REGIONS OF ALAR TRACT BEGAN POSTNUPTIAL
MOLT¹

Region	Rank order ² of beginning of molt
Primaries	1
Upper greater primary coverts	1
Carpal covert	1 or 2
Upper middle primary coverts	3
Under greater primary coverts	6
Under middle primary coverts	5
Secondaries	2
Upper greater secondary coverts	2 or 3
Upper middle secondary coverts	4
Under greater secondary coverts	6 (?) ³
Under middle secondary coverts	7 (?) ⁴
Under lesser secondary coverts	3
Alula	6
Marginal and patagial coverts	3

¹ This table is based on the same birds as those in Table 184.

² Regions with the same rank are believed to begin to molt at about the same time.

³ A few were sheathed on the specimens (one or two) whose primary molt was most advanced; other specimens had full-grown, presumably old, feathers.

⁴ These coverts were full-grown on all specimens; but some showed minute signs of wear, and all were therefore judged old.

below, suggests that sometimes proximal secondaries were shed before any rectrices (male 3) and that sometimes the opposite was true (male 2 and female 2).

Order of beginning of molt within certain tracts.—Alar tract: Table 183 shows the probable order in which the alar tract began to molt using arbitrary ranks numbered 1–7 (earliest to latest). Caudal tract: Upper tail and undertail coverts dropped before rectrices, anal circlet probably shortly after rectrix pair 1. Capital tract: The density and shortness of feathers made determination of sequence difficult. Molt probably began about simultaneously on the anterior frontal and posterior occipital regions, then spread laterally (see Stewart 1952, Foster 1967b: 191, 172). Specimens in advanced molt appeared to have molted this tract in somewhat variable sequence; on all of them the auricular, superciliary, post-auricular, and ocular regions probably molted synchronously. Spinal tract: The center of the dorsal region was the first location to shed feathers, the pelvic region probably the second. Molt quickly spread anteriorly from the midback to the interscapular and cervical regions. Ventral tract: Molt began on the sternal and axillar regions; the interramal region probably started at about the same time. The anterior section of the malar region and the posterior part of the axillar region were quickly involved, followed by the submalar and cervical regions, possibly in that order or possibly simultaneously. The abdominal region molted last.

Progress of molt of remiges and rectrices.—Special attention is given to these feathers because molt was prolonged, can be described with some precision, and has been quantitatively studied in other species (e.g. Newton 1966). Table 184 shows for each sex mean lengths of full grown remiges and rectrices of six specimens, all tower kills in autumn. It then presents data from nine molting specimens, arranged with the most advanced molt at the top. Degree of advancement is judged by number of new primaries of full length; if none was full length, advancement is based on growth of primary 1. O indicates that the old feather

TABLE 184
STATE¹ OF RECTRICES AND REMIGES ON NINE ADULTS IN POSTNUPTIAL MOLT

	Primary number									V ²
	1	2	3	4	5	6	7	8	9	
Mean length when full-grown ³										
Male	39.8	40.9	41.7	42.8	45.3	46.7	45.7	44.6	43.1	
Female	37.3	38.6	39.6	40.7	42.3	43.5	43.0	42.3	41.1	
Male 1	N	N	N	N	N	.9	.8	.6	.3	O
Female 1	N	N	N	N	N	.9	.7	.5	.2	O
Male 2	N	N	N	N	N	.8	.6	.4	.2	O
Male 3	N	N	N	N	.9	.7	.1	O	O	O
Male 4	N	N	N	N	.9	.6	.3	.1	O	O
Male 5	N	N	N	N	.8	.6	.3	.1	O	O
Female 2	N	N	N	.9	.8	.6	.2	O	O	O
Male 6	.9	.7	.5	.1	O	O	O	O	O	O
Male 7	.8	.7	.5	.4	.2	A	O	O	O	O
	Secondary number									
	1	2	3	4	5	6	7	8	9	
Mean length when full-grown										
Male	39.6	39.6	38.8	37.4	35.8	34.3	33.3	28.7	21.8	
Female	35.3	36.8	35.9	34.8	34.0	32.3	31.5	26.3	20.0	
Male 1	N	.7	.5	A	O	O	N	N	N	
Female 1	.9	.7	.5	.2	A	O	N	N	N	
Male 2	.9	.7	.3	O	O	O	N	N	N	
Male 3	.8	O	O	O	O	O	.3	N	N	
Male 4	.9	.8	.2	O	O	O	N	N	.7	
Male 5	.8	.3	O	O	O	O	.2	N	N	
Female 2	.8	.4	A	O	O	O	.9	N	.8	
Male 6	O	O	O	O	O	O	.1	.2	.2	
Male 7	O	O	O	O	O	O	.1	.8	.3	
	Rectrix number									
	1	2	3	4	5	6				
Mean length when full-grown										
Male	47.1	47.6	47.8	48.0	47.3	45.0				
Female	45.3	45.9	45.9	45.7	45.4	43.5				
Male 1	N	N	N	.9	.8	.8				
Female 1	N	N	N	.9	.9	.8				
Male 2	.9	.8	.8	.8	.7	.6				
Male 3	.8	.7	.6	.6	.4	.4				
Male 4	N	N	N	.8	.7	.4				
Male 5	.8	.7	.7	.6	.6	.4				
Female 2	.7	.7	.6	.6	.5	.4				
Male 6	A	A	O	O	O	O				
Male 7	.2	.1	A	A	O	O				

¹ Letters mean the following: N = feather new, fully developed; O = feather old, not yet molted; A = feather absent, no replacement visible. A number means that a developing new feather had attained about that proportion (e.g. .2 = 20%) of its mean length when full grown.

² This is the vestigial 10th primary discussed on page 541.

³ Length is in mm. Each remex and rectrix of 6 males and 6 females killed in autumn in Leon County, Florida, was measured from its base to its tip.

was still present, A that the old feather was absent with no replacement visible, and N that the new feather was of full length. A number indicates a growing feather and shows its length compared with mean length when full-grown.

Primaries and rectrices were renewed centrifugally, secondaries largely cen-

tripetally. For the purpose of comparing the molt of these three groups with respect to synchrony and other patterns of renewal, it seems reasonable to assume either (1) that absolute rate of growth of all an individual's feathers within a group, e.g. primaries, was about the same, or (2) that each feather of a group took about the same number of days to reach full length (compare Newton 1966: 52). On either assumption, we can study differences in length of feathers whose molt sequence is known and obtain useful information about synchrony or other forms of regularity of beginnings of growth. For these comparisons, a difference in length of incompletely developed feathers of a group is a "growth difference"; if the more developed of two feathers that molt in sequence was 0.8 of full length and the less developed was 0.6, the growth difference is 2.

Primaries: Table 184 suggests considerable regularity in intervals separating start of growth of each two adjacent feathers. Seven among 9 molting specimens were renewing 4 primaries each; one specimen had 3 growing primaries and one had 5. The 9 birds tabulated provide 27 growth differences; extremes are 6 and 1, the mean 2.3. The difference between the least developed and the most developed of an individual's primaries is 6 in 3 cases, 7 in 3 cases, 8 in 3 cases.

It will be shown below (pp. 514–515) that the mean growth rate of the rectrices was about 3 mm per day. If the primaries grew at about that rate, a calculation based on Table 184 and using the mean growth difference suggests that 3–4 days separated the beginning of growth of adjacent feathers. This, in turn, may reflect the interval between dropping of two adjacent old feathers (see Watson 1963). If the assumptions of this paragraph are correct, the period between loss of primary 1 and full renewal of primary 9 was some 38–42 days.

Secondaries: Secondary 8 apparently was the first secondary to drop (Table 184); twice in the field I examined males missing only that pair. Most individuals probably next lost 9, then 7 (see Table 184, male 3, male 5, male 6, and male 7); some probably followed the opposite order (male 4 and possibly female 2). Secondary 1 probably sometimes preceded 7 or 9 or both (male 3, male 4, and male 5); and secondary 2, while never more developed than 1, may possibly have begun to grow before 7 or 9 (male 4, male 5). Secondaries 2–6 probably molted centripetally (female 1). Additional evidence that 6 was the last replaced is the fact that on two birds examined in the field only 5 and 6 were still growing, with 6 much less advanced. A female tower kill had completed flight-feather molt except that secondaries 6 were sheathed and a little short.

Individuals at about the same stage of primary molt varied considerably in condition of the secondaries (e.g. male 1, male 2, and female 1); and growth differences between secondaries that probably molted consecutively varied more than differences between primaries (0 in female 2 and male 6, 6 in male 4). The mean of 19 secondary growth differences is 2.8.

Rectrices: The rectrices appeared to be lost centrifugally in at least 50 cases in the field, except that feathers of a pair did not always drop on the same day and occasional birds had only one or two (once four) outer rectrices all on the same side. Replacement was invariably centrifugal. Usually the entire tail dropped within 5–6 days (see discussion p. 514). Assuming a fairly short interval between loss of old feathers and appearance of new (see Watson 1963), Table 184 shows

the synchrony of molt of the rectrices as compared with the other groups of flight feathers. Extreme growth differences of adjacent feathers are 0 and 3, and the mean of 28 cases is 0.8. On four molting specimens (male 2, male 3, male 5, female 2) all rectrices were growing simultaneously; the growth difference between most developed and least developed feathers was only 4 in two instances and only 3 in two instances, or 13–20 mm. In fact, on two museum specimens differences between lengths of growing first and sixth rectrices were only 5 and 6 mm, respectively.

Other progress of molt.—Each upper greater primary covert (including that of vestigial primary 10) evidently dropped just before its primary; on some molting specimens the old primary was overlain by a new covert 1–2 mm long. The covert reached full development more rapidly than its primary; no molting specimen had more than two greater coverts growing simultaneously, and some had only one. Upper middle primary coverts were molting on six of the specimens; progress was distinctly centripetal in some cases; but the coverts of others were of equal length, and on another specimen length appeared to vary randomly.

The under greater primary coverts of two specimens were molting centrifugally. The under middle primary coverts of 4 were in molt, the sequence highly variable: on 1, molt appeared centrifugal; on 2, old feathers and sheaths seemed randomly interspersed; on 1, replacement of all coverts appeared simultaneous.

The upper greater secondary coverts were of equal length on all molting specimens on which these coverts were being renewed. The upper middle secondary coverts on four consisted of old and growing new feathers distributed apparently randomly; a fifth bird showed a centripetal tendency.

Only one, possibly two, molting specimens had sheathed under greater secondary coverts, their sequence of molt not clear. On one specimen the under middle secondary coverts were the only feathers of the alar tract still in molt; they were of equal length. Molt sequence of the under lesser secondary coverts appeared variable, on three specimens distinctly centripetal, on one approximately simultaneous, on another apparently random.

The alula was molting on 2 specimens, both of which retained the largest, distal feather; 1 had lost the other 2 feathers and 1 only the most proximal feather. Thus this molt is centrifugal.

On both ventral and dorsal surfaces of the forearm, molt began nearest the body at the anterior edge of the wing and proceeded distally and posteriorly; dorsal feathers on some molting specimens appeared more developed than ventral. The marginal coverts of the hand apparently began to molt about simultaneously with the forearm but did not progress centrifugally; no sequence was detected.

On three molting specimens upper tail coverts were growing and of equal length; another was renewing most coverts simultaneously but retained some old feathers in no symmetrical pattern. In contrast to these four individuals, on three specimens whose coverts were about full length but were more or less sheathed, sheath lengths suggested centripetal molt. The state of undertail coverts indicated great individual variation including simultaneous loss, random order of loss, loss of all coverts on one side before any on the other, and centrifugal loss.

TABLE 185
REGIONS UNDERGOING POSTNUPTIAL MOLT ON AUTUMN MIGRANTS¹

Region	N	As % of 167 molting specimens	N molting only on indicated region	N molting on indicated region and other region(s)
Auricular	87	52	46	41
Occipital	65	39	4	6
Sternal	43	26	2	41
Submalar-cervical	34	20	0	34
Coronal-superciliary	29	17	1	28
Axillary	23	14	0	23
Mid-dorsal	20	12	0	20
Abdominal	18	11	1	18
Cervical-intercapular	9	5	0	10
Interramal	9	5	0	9
Pelvic	5	3	0	5
Upper tail coverts	5	3	0	5
Undertail coverts	4	2	1	3
Malar	4	2	0	4
Frontal	2	1	0	2

¹ The birds were killed during nocturnal migration through Leon County, Florida; 91 of 141 males and 76 of 101 females were molting. Regions in molt did not differ according to sex, and the sexes are pooled. Dates of death are presented in Chapter 36; the association between date and end of molt is referred to on page 516 and analyzed in Table 186.

On the capital, spinal, and ventral tracts molt appeared to begin medially and spread laterally. This applies to progression from region to region and it also appears true within single regions that were large enough to permit me to detect a sequence.

Molt of the humeral tract began anteriorly. Two specimens in early molt showed no evidence of a lateral spread concurrent with the posterior spread; i.e. sheathed feathers of equal length were distributed across the anterior end of the tract. On a third specimen molt appeared to progress proximally to distally as well as from anterior to posterior.

The femoral tract molted either proximally to distally or toward both margins from a medial origin. Whether replacement also proceeded posteriorly was not clear; on four molting specimens such a progression was evident, but two birds probably had molted anterior feathers first.

Crural molt probably began below the knee and progressed both proximally and distally, involving the feathers near the heel last.

Completion of molt.—Mumford and I found molt still in progress but in late stages on 167 adult autumn tower kills. Table 185 shows the regions involved, with the sexes pooled because they did not differ. One bird had sheathed flight feathers (secondaries 6); the rest were molting only on head or body (compare Orange-crowned Warbler, Foster 1967b: 190). The variety of locations still molting suggests that most regions of the head and body tended to finish at about the same time, with the auricular and/or occipital region usually last; of 87 tower kills still in auricular molt, 46 were molting only there (compare Foster 1967b: 190).

POSTNUPTIAL MOLT: DURATION

Methods.—The phase during which molt was observable in the field is the "noticeable molt."

A few banded individuals were found regularly throughout noticeable molt, thus providing measures of its length; but many were observed repeatedly only during some part of it. Therefore I have divided noticeable molt into arbitrary stages; the approximate duration of each stage is known for at least 10 individuals. The sum of mean lengths of these stages produces a composite that is consistent with observed durations on the few individuals seen throughout the molt. No sexual difference was observed, and data for males and females are pooled.

Noticeable molt in birds without dependent young.—The mean length of noticeable molt based on composite data was 39–42 days, and 5 individuals observed during the full noticeable molt took about 40 days.

The usual period from first observable loss of body and/or head feathers until first shedding of rectrices was 2–8 days (mean 6); it then took 2–7 days (mean 5) until all rectrices were lost; 18–20 days elapsed until rectrix pair 1 was full grown, and the outer pair or pairs of rectrices usually were full grown 3–4 days later; for about 10 more days molt was evident on the head, after which the new plumage appeared complete. An individual passing through each stage in minimum time would be in noticeable molt 35 days; the opposite extreme is 49 days.

The interval between end of noticeable molt until completion of molt is unknown. Banded birds often remained on the study area for a month or so after noticeable molt finished. That fact and the fact that many migrant tower kills were still molting slightly make it likely that molt continued at least 10–15 days after it ceased to be noticeable.

Noticeable molt in birds with dependent young.—No adult tending a late brood molted at the rate just described for birds without young. In 11 females (yearling and older) and 2 males, all caring for young, the time between start of noticeable molt and first loss of rectrices was 15–37 days; one additional female parent took 15 days to lose her tail after shedding rectrix pair 1. (That only two males delayed molt is probably the result of my finding more females than males caring for young late in the season; see p. 429.) I detected molt on most of these 14 birds while they were feeding nestlings or new fledglings, and the prolonged period required for the rectrices to drop coincided with the first weeks the fledglings were out of the nest. Others of these 14 started to show molt while incubating, then either made no apparent progress after the eggs hatched or molted very slowly. In all cases in which molt was retarded, it appeared to resume at the normal pace after the tail had dropped. I assume that this delaying of molt of the tail probably also involved other flight feathers, i.e. that primary molt was interrupted, but that could not be detected in the field.

Newton (1966: 48, 52–53) reported that molt of the Bullfinch is delayed during feeding of dependent young and suggests that this “could have been directly due to ‘shortage’ of food imposed by the dual strain of molt and parental care” (see also Miller 1961, Newton 1966: 55–56; but see Newton 1968). The general resemblance between Newton’s results and mine is striking; however, he netted systematically and obtained more precise and extensive information, including data about delay in primary molt.

Daily growth of rectrices.—If it is assumed that 2–3 days passed between dropping a rectrix and appearance of the incoming sheath (this is true of a few

TABLE 186
EXTENT OF POSTNUPTIAL MOLT ON MIGRANTS THROUGH FLORIDA,¹
ACCORDING TO SEX AND DATE

Extent of molt ²	1-15 August	16-31 August	1-15 Sept.	16-30 Sept.	October
Males					
None	0	5	12	21	12
Light	1	38	15	17	10
Moderate	1	6	1	1	0
Heavy	0	1	0	0	0
Totals	2	50	28	39	22
Still molting					
N	2	45	16	18	10
%	100	90	57	46	45
Females					
None	1	4	7	10	3
Light	0	30	12	9	11
Moderate	1	8	0	0	0
Heavy	1	2	1	0	1
Totals	3	44	20	19	15
Still molting					
N	2	40	13	9	12
%	67	91	65	47	80

¹ The birds (all adult) were killed in nocturnal collisions with a television tower in Leon County, Florida.

² Light molt consists of the presence of a few growing feathers on no more than 2 regions; heavy molt is the presence of many growing feathers on at least 2 regions; moderate molt is intermediate. All birds in heavy molt had sheathed feathers on both the head and the body.

passerines whose rectrices I have pulled), the mean daily growth rate of a rectrix is a little less than 3 mm; compare Newton (1966: 47). The rate from day to day appeared fairly constant. Application of a daily 3-mm rate to the rectrices of molting specimens in Table 184 yields results consistent with field observations. To illustrate, the lengths of male 3's rectrices suggest a 6-7 day period between start of growth of pair 1 and pair 6. The museum specimens (see p. 512) whose most and least developed rectrices differed in length by only 5-6 mm appear to correspond to study-area birds that lost the entire tail in 2 days.

POSTNUPTIAL MOLT: DATES AND TIMING

I know or can calculate approximate dates of beginning of molt of 73 males and 73 females, counting individuals once for each year they were studied; calculations assume that birds observed in midmolt had molted at normal rates prior to the observation.

In analyzing for a possible relationship between date of beginning of molt and date at which reproduction ended, I took into account the difference in time required to drop the rectrices in birds that were and that were not tending young. To standardize treatment of these two groups I calculated the molt of both as having begun 11 days before the last rectrices were lost (see p. 514). This ignored the prolongation of early stages of molt in parents of fledglings.

The earliest date at which noticeable molt began on the study area was 25 June, the latest 8 September. The mean date of 146 cases was 25.1 July (SD 14.2 days). I have seen museum specimens of adult males, all from Maryland,

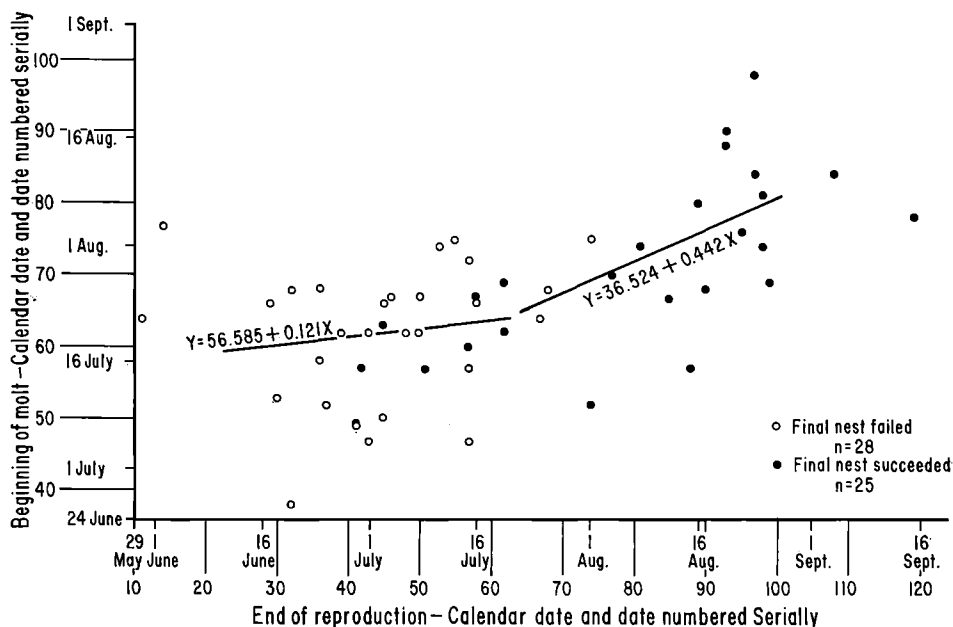


FIGURE 41. Relation of date of onset of molt of males to date of end of reproduction, according to whether the final nest succeeded or failed. Dates are shown as calendar dates and as a series (used in the regressions) in which 1 = 20 May. In the regression equations, Y intercept 36 = 24 June and Y intercept 56 = 14 July.

in full postnuptial plumage when collected on 30 July, 3 August, and 4 August (two cases); these birds probably began noticeable molt in mid-June (see p. 514).

Dates of onset according to sex.—Extreme dates of beginning of noticeable molt in males were 1 July and 17 August. The mean of the 73 cases was 24.3 July (SD 12.0 days). Extreme dates for females were 25 June and 8 September; two or perhaps three females were still in noticeable molt in October. The mean of the 73 cases was 25.9 July (SD 16.2 days); note the greater variance as compared with males. A higher proportion (nonsignificant) of females killed while migrating through Florida was still molting; among October kills most females were in molt whereas most males were not (Table 186). Thus field observations and tower data suggest that while the mean dates for the sexes are about the same, more females than males molt very early and very late.

Onset of molt and end of reproduction.—Figures 41 and 42 show for each sex dates of beginning of molt plotted against dates of end of reproduction; individuals whose reproduction ended with failure of the last nest are treated separately from those that finished reproduction by bringing fledglings to independence.

To consider first those birds whose last nests failed, 28 males began to molt on the mean date 20.0 July, (SD 9.7 days), after nest failures on the mean 2.8 July; the two dates were not correlated ($r = 0.18$, $df = 26$). The situation with females was quite different: Only 10 females that failed to reproduce remained on the study area and were seen during molt (see Chapter 35); the last nests of these failed on the mean 10.4 July, and molt began on the mean 15.0 July

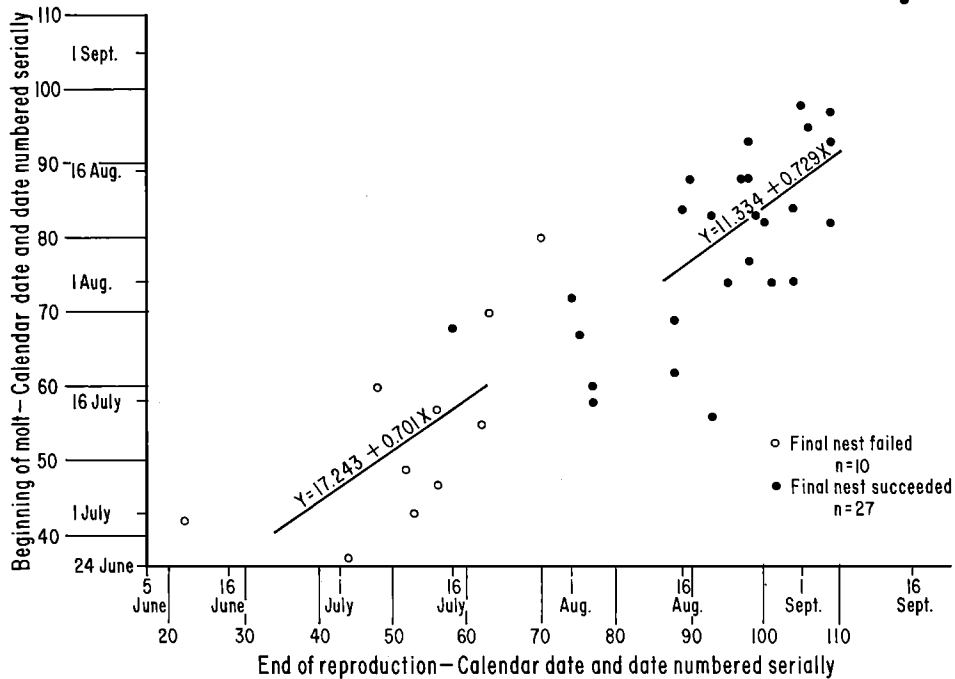


FIGURE 42. Relation of date of onset of molt of females to date of end of reproduction, according to whether the final nest succeeded or failed. Dates are shown as calendar dates and as a series (used in the regressions) in which 1 = 20 May. In the regression equations, Y intercept 11 = 30 May and Y intercept 17 = 5 June.

(SD 13.7 days); $r = 0.71$; $df = 8$; $P < 0.05$. I interpret the correlation in females and its absence in males as follows: Females that lost nests and that remained on the study area without rebuilding or pairing again were almost certainly no longer in breeding condition, and the data indicate a positive correlation between loss of reproductive condition and onset of molt; the brevity of the period between nest loss and molt may even suggest an acceleration of start of molt as the result of the end of reproduction. Many of the males whose mates disappeared after nest failure were themselves still in breeding condition; some gained new mates but many did not (Chapters 31 and 34). Thus the date a male's reproduction ended was often related not to his but his mate's condition, and no correlation with onset of molt would be expected in males.

Among parents of fledglings, 25 males tended young until independence, which fell on the mean date 5.8 August; they began to molt on 30.6 July (SD 15.7 days); $r = 0.81$; $df = 23$; $P < 0.01$. For 27 females, the mean date of independence of young was 21.5 August, the mean date of beginning of molt 7.1 August (SD 13.6 days); $r = 0.71$; $df = 25$; $P < 0.01$ (compare Welty 1962: 41-42, Newton 1966: 49, 55-56, Foster 1967b: 191-193). The difference in mean dates of independence of young tended by males and females appears to have resulted from factors irrelevant to the present subject (see p. 429).

In a test of significance of the difference between mean date of onset of molt of males whose last nests failed and of males that tended fledglings, $t = 2.99$;

df = 51; $P \cong 0.005$. In a test on the two groups of females, $t = 4.58$; df = 35; $P < 0.001$. These differences point to a mechanism tending to reduce overlap between the energetic demands of reproduction and molt. The incompatibility of caring for fledglings and molting is suggested by the sharp contrasts between parental behavior (pp. 322–323) and behavior during molt (p. 435); see also the comments of Newton (p. 514) as well as studies of metabolic differences between molting and nonmolting birds (e.g. Lustick 1970).

Variation in onset, according to age.—Among adults (both sexes) whose ages and molt dates I knew were 28 yearlings and 46 old birds. Extreme dates of start of molt of yearlings were 25 June and 15 August, the mean 15.4 July (SD 14.8 days). Extremes for old birds were 10 July and 8 September, the mean 31.1 July (SD 12.7 days). In a test of significance, $t = 4.84$; df = 72; $P < 0.001$. Among 15 birds of known age that began to molt earlier than 15 July, 13 were yearlings; among 7 that began on or after 15 August only 1 was a yearling.

As discussed earlier, yearlings probably quit replacing failed nests at an earlier date than old females quit (pp. 423–424). The age difference just shown in onset of molt may have been entirely or partly attributable to a difference in date of end of reproduction of the birds tested (compare Newton 1966: 49, Foster 1967b: 193, Snow 1969). Support for this suggestion comes from comparisons of age classes broken down according to reproductive success. Among unsuccessful individuals, 14 yearlings began to molt on 7.1 July (SD 10.8 days); 17 old birds began on 24.9 July (SD 6.2 days); $t = 5.75$; df = 29; $P < 0.001$. In a comparison of dates for 11 successful yearlings and 29 successful older adults, t is nonsignificant. (For some yearlings, the outcome of reproduction was not known.)

Dates of molt in individuals in successive years.—Molt dates of individuals in different years varied with their reproductive success in these years. Representative examples follow: (1) A female that brought off young rather late in one season began to molt 11 August—16 days later than that year's mean molt date for the population as a whole. Next year her last nest failed early, and she began to molt 16 July—19 days before that year's mean date. (2) Similarly, varying dates of end of reproduction were correlated with a male's molt dates, which were 23 days before, 7 days after, and 1 day before the population's mean dates in 3 years. (3) A female began to molt 34 days after, 15 days after, and 29 days after annual mean dates, but in all cases 2–10 days before her broods became independent. (4) A male whose reproduction ended quite early in successive years began to molt on 24 July and 25 July.

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Museums that assisted me are named on page 360. I thank them and their directors. Appendix 1 acknowledges the assistance of a great many correspondents who generously provided information about the Prairie Warbler's local distribution.

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APPENDIX 1

DETAILS OF PRESENT BREEDING RANGE

The range map on page 7 is based largely on information obtained in 1965. Major state and regional works of that date (all are listed in the bibliography in Pettingill 1970: 473–481) were consulted; but for most states and for Ontario, correspondence with active field workers was relied on for details of local distribution. Information so obtained has been supplemented by data from the U.S. Fish and Wildlife Service's 1967 Breeding Bird Survey (kindly supplied by Chandler S. Robbins) and by more recent state works (e.g. Bull 1974).

Despite the generous contributions of so many correspondents, it is clear that for certain states Figure 4 does no more than suggest the Prairie Warbler's current distribution. (1) Particularly in states subdivided into many counties, local information is insufficiently detailed. (2) Status as a breeding species is often inferred merely from the presence of singing males, although in some cases such males were present in large numbers and were recorded over several years. (3) The Prairie Warbler's range has extended so rapidly since 1900 that we cannot assume that even a map accurate when prepared remains current. On the other hand, urbanization and reforestation have certainly eliminated the species from localities where it was numerous only a few years ago.

The following lists alphabetically, by states, and within states by counties, counties in which the Prairie Warbler is believed to breed. No attempt has been made to exclude counties recently occupied by the bird but now probably totally urbanized. Counties in which correspondents suspected breeding solely on the basis of the presence of suitable habitat and the proximity of breeding colonies were not shown on the map but are listed below appropriately designated. Following the information from each state are the names of the local experts who helped me. If I have misinterpreted any of the many maps, lists, and other communications that they so kindly sent me, the responsibility is mine.

Alabama—All except possibly Baldwin and Mobile (Thomas A. Imhof).

Arkansas—Baxter, Benton, Boone, Carroll, Clark, Cleburne, Columbia, Conway, Crawford, Faulkner, Franklin, Fulton, Garland, Grant, Hempstead, Hot Spring, Howard, Independence, Izard, Jefferson, Johnson, Lafayette, Lawrence, Little River, Logan, Lonoke, Madison, Marion, Miller, Montgomery, Nevada, Newton, Ouachita, Perry, Pike, Polk, Pope, Pulaski, Randolph, Saline, Scott, Searcy, Sebastian, Sevier, Sharp, Stone, Union, Van Buren, Washington, White, Yell (Ben B. Coffey, Jr., Douglas James, Merritt G. Vaiden).

Connecticut—All (Robert DeWire, Dean H. Kelsey, James Orcutt, Maynard W. Peterson, Noble S. Proctor, James A. Slater).

Delaware—All (David A. Cutler, Samuel H. Dyke).

Florida—*D. d. discolor*: Gadsden, Holmes, Jackson, Leon, Okaloosa, Santa Rosa, Walton, *D. d. paludicola*: Brevard, Broward, Charlotte, Citrus, Collier, Dade, Duval, Flagler, Hernando, Hillsborough, Indian River, Lee, Levy, Manatee, Martin, Monroe, Palm Beach, Pasco, Pinellas, St. Johns, St. Lucie, Sarasota, Volusia, and possibly Dixie (David W. Johnston, William B. Robertson, Jr., Henry M. Stevenson).

Georgia—All except Atkinson, Bacon, Brantley, Brooks, Camden, Charlton, Clinch, Cook, Decatur, Echols, Glynn, Lamar, Lowndes, Pierce, Ware, and possibly except Appling, Baker, Berrien, Calhoun, Coffee, Colquitt, Dougherty, Jeff Davis, Long, McIntosh, Miller, Mitchell, Seminole, Thomas, Tift, Turner, Wayne, Worth (Mrs. Thomas J. Cater, Jr., J. Fred Denton).

Illinois—Alexander, Calhoun, Clinton, Cook, Gallatin, Hardin, Jackson, Jersey, Johnson, Livingston, Madison, Massac, Monroe, Perry, Peoria, Piatt, Pope, Pulaski, Randolph, Richland, St. Clair, Saline, Union, Washington, Will, Williamson (Richard R. Graber, Vernon M. Kleen, E. J. Wilhelm, Jr.).

- Indiana—Brown, Clark, Clay, Crawford, Dubois, Fayette, Floyd, Franklin, Gibson, Greene, Hamilton, Harrison, Jackson, Jefferson, Lake, Lawrence, Marion, Martin, Monroe, Morgan, Orange, Owen, Parke, Perry, Pike, Porter, Ripley, Spencer, Sullivan, Switzerland, Union, Vanderburgh, Warrick, Wayne and probably Bartholemew, Daviess, Dearborn, Decatur, Hancock, Henry, Jennings, Johnson, Knox, Ohio, Posey, Putnam, Scott, Vigo, Washington (Holly Reed Bennett, John F. Branham, James B. Cope, Charles Keller, Russell E. Mumford).
- Iowa—No satisfactory evidence of breeding despite several old reports; see Anderson (1907: 357). (Karl E. Goellner, Peter Petersen, Jr., William Youngworth).
- Kansas—Cherokee, Johnson, Wyandotte (James D. Rising).
- Kentucky—All but Adair, Allen, Anderson, Ballard, Barren, Bourbon, Carlisle, Cumberland, Fayette, Fulton, Green, Hickman, Jessamine, McCracken, Metcalfe, Monroe, Russell, Simpson, Spencer, Trigg, Washington, Woodford (Roger Barbour, Robert M. Mengel).
- Louisiana—Bienville, Bossier, Caddo, Caldwell, Claiborne, DeSoto, East Baton, East Feliciana, Grant, Jackson, LaSalle, Lincoln, Livingston, Natchitoches, Ouachita, Rapides, Red River, St. Helena, St. Tammany, Tangipahoa, Union, Washington, Webster, West Feliciana, Winn (George H. Lowery, Jr.).
- Maine—York. (Christopher M. Packard).
- Maryland—All (Maurice Brooks).
- Massachusetts—All (Edith Andrews, James Baird, Stanwood K. Bolton, Jr., Davis H. Crampton, Samuel Eliot, Bart Hendricks, Allan Keith).
- Michigan—Berrien (formerly), Crawford, Muskegon, Oceana, Oscoda, Otsego, Ottawa, Presque Isle, Sheboygan, and possibly Alger, Allegan, Marquette, Schoolcraft (Douglas S. Middleton).
- Mississippi—Adams, Alcorn, Attala, Benton, Calhoun, Carroll, Chickasaw, Choctaw, Clarke, Clay, Granada, Holmes, Itawamba, Jefferson Davis, Jones, Kemper, Lafayette, Lamar, Lauderdale, Leake, Lee, Leflore, Lowndes, Marshall, Monroe, Montgomery, Neshoba, Newton, Noxubee, Oktibbeha, Pearl River, Pontotoc, Prentiss, Tippah, Tishomingo, Union, Wayne, Webster, Winston, and possibly Jasper, Madison, Scott, Yalobusha (Ben B. Coffey, Jr., B. E. Gandy, Merritt G. Vaiden).
- Missouri—Barry, Boone, Camden, Christian, Cole, Franklin, Jefferson, Lincoln, Maries, McDonald, Morgan, St. Charles, St. Francois, St. Louis, Ste. Genevieve, Shannon, Stone, Taney, Texas, Washington, Wayne, and possibly Barton, Bates, Benton, Bollinger, Butler, Calloway, Cape Girardeau, Carter, Cedar, Cooper, Crawford, Dade, Dallas, Dent, Douglas, Gasconade, Greene, Hickory, Henry, Howard, Iron, Jasper, Johnson, Laclede, Lawrence, Madison, Miller, Moniteau, Montgomery, Newton, Oregon, Osage, Ozark, Perry, Pettis, Phelps, Polk, Pulaski, Reynolds, Ripley, St. Clair, Vernon, Warren, Webster, Wright (Richard Anderson, J. Earl Comfort, David A. Easterla, William H. Elder, N. Irving Fay, Paul Heye, Spencer Jones, John H. Rogers, E. J. Wilhelm, Jr.).
- Nebraska—Mid-19th century records from Dakota, Lancaster, and Richardson counties evidently have never been repeated; see Bruner *et al.* (1904) and Rapp *et al.* (1958: 26). (Doris Gates; J. Knox Jones, Jr., Willetta Lueshen, William F. Rapp, Jr.).
- New Hampshire—Belknap, Carrol, Cheshire, Hillsboro, Merrimack, Rockingham, Strafford, and possibly Sullivan (Vera Hebert).
- New Jersey—All but Mercer and possibly Essex, Hudson, Union (Vincent Abraitys, Irving H. Black, James L. Edwards, Alfred E. Eynon, George Komoroski, Frank W. McLaughlin, Bertram G. Murray, Jr., Farris S. Swackhammer).
- New York—Albany, Broome, Cattaraugus, Cayuga, Chemung, Columbia, Dutchess, Essex, Nassau, Orange, Oswego, Putnam, Rockland, Suffolk, Tompkins, Westchester, Yates, and possibly Oneida (Harold H. Axtell, Allen H. Benton, John Bull, Stephen W. Eaton, Ralph Palmer, Sally F. H. Spofford, Walter R. Spofford).
- North Carolina—All (John Wallace Coffey, Harry T. Davis).
- Ohio—Adams, Athens, Coshocton, Fairfield, Gallia, Greene, Hamilton, Highland, Hocking, Jackson, Lawrence, Meigs, Morgan, Muskingum, Perry, Pike, Ross, Scioto, Vinton (Donald J. Borrer, Jay M. Sheppard, Tom E. Shields, Edward S. Thomas).
- Oklahoma—Caddo, Cherokee, Cleveland, Delaware, Hughes, Latimer, LeFlore, Logan,

- McCurtain, Mayes, Murray, Muskogee, Ottawa, Pottawatomie, Pushmataha, Sequoyah, Tulsa, Wagoner (F. M. Baumgartner, George M. Sutton).
- Ontario—Bruce, Frontenac, Lambton, Muskoka, Norfolk, Simcoe, Victoria (James L. Baillie, Jr., Jon C. Barlow).
- Pennsylvania—Adams, Armstrong, Beaver, Bedford, Berks, Bucks, Butler, Centre, Chester, Cumberland, Fayette, Fulton, Greene, Huntingdon, Indiana, Lancaster, Lebanon, Monroe, Montgomery, Perry, Schuylkill, Union, Westmoreland, York, and probably Delaware and (formerly) Philadelphia (Maurice Brooks, Mary H. Clench, David A. Cutler, Robert C. Leberman, Earle F. Poole, C. Chandler Ross, Phillips B. Street).
- Rhode Island—All (James Baird, Katherine B. Kinsey, D. L. Kraus, Merrill E. Slate, Charles Wood).
- South Carolina—All (B. Rhett Chamberlain).
- Tennessee—Benton, Blount, Cannon, Carter, Carroll, Cheatham, Chester, Clay, Cocke, Coffee, Cumberland, Davidson, Decatur, Dickson, Fayette, Fentress, Gibson, Greene, Hamilton, Hardeman, Hardin, Henderson, Henry, Hickman, Humphreys, Johnson, Knox, Lawrence, Lewis, Loudon, McMinn, McNairy, Marion, Montgomery, Perry, Putnam, Robertson, Rutherford, Sevier, Sullivan, Trousdale, Van Buren, Wayne, White, Williamson (Ben B. Coffey, Jr., John Wallace Coffey, Eugene Cypert, J. C. Howell, Amelia R. Laskey, Arthur Stupka).
- Texas—Anderson, Cherokee, Nacogdoches, Rusk, Smith, and possibly Cass, Gregg, Harrison, Marion, Panola, Upshur (O. C. Sheffield).
- Virginia—All except possibly Highland (John Wallace Coffey, Jr., J. J. Murray).
- West Virginia—All (Maurice Brooks).

APPENDIX 2

DESCRIPTIONS OF BREEDING HABITATS

SOUTHERN PINE FORESTS

Locations.—The coastal plain in southeastern North Carolina, South Carolina (Sprunt and Chamberlain 1949: 40), Georgia, western Florida; in scattered areas west to Oklahoma and Texas (Shelford 1963: 81).

Description.—Characteristically open (see Norris 1951: 40), admitting sunlight and permitting growth of a shrub layer. A Georgia forest censused by Aldrich and Burleigh (1946) contained Sweet and Black Gum; oak species are also usually present. Characteristic bird species in southeastern pine forests include the Red-cockaded Woodpecker, Brown-headed Nuthatch, Pine Warbler, Indigo Bunting, Bachman's Sparrow.

Duration.—A pine forest inhabited by Prairie Warblers in Georgia was considered relatively mature (Aldrich and Burleigh 1946) at age 50–60 years; trees were about 27 m high. Intermittent destruction by natural (Kendeigh 1961: 117) and intentionally set fire arrests succession and maintains this pine subclimax; Prairie Warblers probably enter the forest a few years after a fire and remain until the shrub layer is again burned off.

SAND DUNES

Location.—Along the Atlantic coast, especially in Virginia, the Carolinas, and Georgia (Pearson *et al.* 1919: 298, Poole 1923, Duvall 1937, Sprunt and Chamberlain 1948: 469, Burleigh 1958: 539), also along Lake Michigan in Indiana and Michigan. In Ontario, the Prairie Warbler inhabits "juniper clumps on sand dunes" along Lake Huron and Georgian Bay (James L. Baillie pers. comm., Snyder 1951: 200).

Description.—The dry substrate is unusually hot during the day and cold at night; its surface is irregular and often undulating; strong winds are frequent, and dunes are therefore unstable where grasses have not temporarily bound the sand. Common trees are pine species, Cottonwood, and oak species. Shrubby plants are often growing in a sparse, open, exposed belt, at times as narrow as 35 m (pers. obs., Scott Rea pers. comm.); Prairie Warbler territories are frequently arranged linearly along this belt. Associated species in Indiana are the Mourning Dove, Eastern Kingbird, Vesper Sparrow, Chipping Sparrow, Field Sparrow.

Duration.—Olson (1958: 139, 140) indicates the shrub stage in the Indiana dunes lasts several decades; but erosion, sand migration, and changes in water level lead to steady renewal of the shrub habitat (see Waterman 1928: 104) which therefore may be present indefinitely.

MANGROVES

Location.—Florida, north to Brevard County on the east coast and to Citrus County on the west; scattered mangroves also occur somewhat farther northward.

Description.—Dominated by one or some combination of Red Mangrove, Black Mangrove, and White Mangrove; Buttonbush is often associated. As described by Robertson (1955: 362), Prairie Warblers inhabit "... extensive areas with a plant cover characterized by bush-sized [Red Mangrove] and [Black Mangrove]. These stands vary greatly in density. Some sites have nearly continuous stands of low bushes. Elsewhere the stand consists of widely scattered bushes with interspersed areas of bare salt flats, low shrubby or herbaceous halophytes, or open water." In one stand, Prairie Warblers were found breeding with 13 other bird species, 9 of these aquatic nonpasserines (Robertson *op. cit.*: 424). Also sometimes associated is a race of the Yellow Warbler, *Dendroica petechia gundlachi* (Robert P. Allen pers. comm.).

Duration.—Robertson (1955: 272) reports an instance in which a new mangrove community took 30–40 years to reach the closed-forest stage. However, as with dunes, various forces constantly renew mangrove habitat, which therefore would normally be present indefinitely.

JACK-PINE PLAINS

Location.—Northern part of the lower peninsula of Michigan.

Description.—Sandy soil with little or no humus; ground cover sparse; much soil bare. Deciduous woody plants are scrubby oak species, Quaking Aspen, cherries, Shadbush. Important associated bird species include Black-capped Chickadee, Brown Thrasher, Kirtland's Warbler, and Chipping Sparrow. Mayfield (1960: 9–23) has described these plains in detail.

Duration.—The Jack-Pine dominant owes its continued existence to forest fire. Prairie Warblers invade when pines are about 1 m high (Mayfield pers. comm.), i.e. about 5 years after a fire. Based on personal communications, I estimate that the species inhabits Jack-Pines about 18 years (see Kammeraad 1963, 1964).

OTHER PINE SUBCLIMAXES

Location.—In the eastern United States are numerous "barrens," dry, burned-over, flat, sandy tracts supporting stunted pines and/or scrubby oaks (see Oosting 1950: 225–256). Barrens are commonest in the coastal plain, but are found in New England, near Albany, New York (Bedell 1940), near State College, Pennsylvania, and elsewhere. Oak shoots often grow very densely from tree roots after older growth has been killed back.

Description.—An example from Long Island, New York (Conard 1935: 476–479) had a low tree layer of Pitch Pine covering 25–50% of the quadrat studied; a low shrub layer of oaks, huckleberries, ferns, and other plants covered more than 25% of the shrub-level plane; the ground layer covered 25–50% of the surface. Common associates of the Prairie Warbler on the eastern barrens are the Whip-poor-will, Great Crested Flycatcher, House Wren, American Robin, Pine Warbler, Common Yellowthroat, Rufous-sided Towhee, Chipping Sparrow, and Field Sparrow.

Duration.—The period of suitability for Prairie Warblers varies with local conditions and frequency of fire. Fables (1938) began observations in the New Jersey Pine Barrens about 8 years after a fire. Trees were denser in the burned part than in the unburned; young Pitch Pines were slightly more than 2 m high, oaks shorter. About 8–10 years later the pines were over 4 m high, the oaks almost unchanged (Fables 1947); after 2 more years, the pines were very dense with little open space left (Fables 1949). Prairie Warblers probably entered this tract about 5 years after the fire, reached maximum density about 10–12 years after entry, and probably disappeared after some 20 years of occupation (see Fables 1954).

ABANDONED FIELDS

Location.—Throughout the breeding range of the race *discolor*.

Descriptions.—Connecticut examples: (1) Pastureland had been abandoned for an unstated length of time; "semi-open fields and shrubland" supported scattered large oaks, sumacs, various small saplings, bayberry, and other brushy growth; dense thickets grew along old stone fences (Kashanski and Niering 1955). Associated with the Prairie Warbler were the Gray Catbird, White-eyed Vireo, Chestnut-sided Warbler, Common Yellowthroat, and Rufous-sided Towhee. (2) A hillside pasture, 75% grass covered and still lightly grazed, was grown up with hawthorns as high as 5 m and clumps of Japanese Barberry about 1 m tall (Magee and Enders 1965, Magee and Cavanaugh 1966). Other small trees and shrubs were conifers, cedar, and laurel. The five commonest birds, in descending order, were Song Sparrow, Prairie Warbler, Field Sparrow, Blue-winged Warbler, and American Woodcock. Georgia example: In terraced fields in the Piedmont, the woodier growth was on the terraces (Johnston and Odum 1956). About 35% of a field abandoned about 20 years earlier was covered with Loblolly Pine, deciduous trees up to 8 m high, and Blackberry thickets as high as

about 2 m. *Andropogon* and other grasses and herbs dominated the inter-terrace areas. In a 25-year-old field, open grassy plots still comprised 44% of the area; thickets covered 23%, Shortleaf and Loblolly Pine 33%. Prairie Warblers were breeding in equal density in these two fields, but were absent in fields abandoned 15 years and 35 years previously. Important associates were Common Yellowthroat, Yellow-breasted Chat, and Field Sparrow. North Carolina example: In the Piedmont Prairie Warblers were common in shrubby fields where pines were 1–20 years old but rarely entered plots of older pines (Oelke 1966a, 1966b, 1966c, 1966d, 1966e). Tennessee example: Fifteen years after depopulation of cultivated land in connection with the establishment of an atomic energy plant, Shortleaf Pine, Jersey Pine, Red Cedar, and Sassafras were common invading trees; the shrubs *Rubus*, *Rosa*, *Smilax* were also numerous (Howell 1958). The Prairie Warbler entered about the 7th or 8th year after abandonment, in the 15th year was the fourth commonest bird (after the Cardinal, Yellow-breasted Chat, and Indigo Bunting). Examples elsewhere: Dry oak-hickory scrub (sometimes associated with pines), similar to the vegetation at the interface of the forest and grassland biomes, is a successional stage in some abandoned-field and cut-over forest seres in Illinois (Richard Brewer pers. comm., Cahn and Hyde 1929), Oklahoma (F. M. Baumgartner pers. comm.), Arkansas (Douglas James pers. comm., Hoiberg 1953, Hoiberg and Hoiberg 1953), Missouri (Widman 1907: 232), Kansas (R. Johnston 1960: 52, Elizabeth L. Cole pers. comm.), and Louisiana (Lowery 1960: 443). Prairie Warblers inhabit this stage.

GRASSLAND—FOREST CONTACTS

Location.—An ecotone of 4 million ha distributed in patches extends westward 1600 km from its eastern limits in Ohio and reaches from 30° N to 48° N (Shelford 1963: 306–307).

Description.—Oak species, Black Walnut, Hackberry, hickory species, and Basswood dominate. Important shrubs include Redbud, *Malus*, *Crataegus*, *Cornus* species, *Rhus* and *Rosa* vines; briars are prominent. *Andropogon*, *Poa*, and *Solidago* are also characteristic (Shelford 1963: 309–313). At the edge of the forest and along streams in the grasslands, this community occurs as a zone of low trees and shrubs in belts 3–10 m wide. Common birds are Yellow-billed Cuckoo, Gray Catbird, Brown Thrasher, Indigo Bunting, American Goldfinch, Chipping Sparrow, and Field Sparrow.

Duration.—Indefinite; succession produces slow shifts in the location of forest-edge growth but not its disappearance; there is “constant fluctuation back and forth with changes in climate” (Shelford 1963: 306).

APPLE ORCHARDS

Cultivated orchards apparently are inhabited only under unusual conditions, when population density is very high (pp. 15–16), probably as in Maryland (Springer and Stewart 1948) and adjoining sections of West Virginia (DeGarmo 1949); see Chapter 1. Neglected or abandoned overgrown, shrubby orchards are inhabited in Indiana and doubtless throughout the range.

STRIP-MINED LANDS

Location.—Prairie Warblers inhabit strip-mined areas in Indiana, Illinois (Richard Brewer pers. comm.), Pennsylvania (Harrison 1964), and probably elsewhere.

Description.—The overturned substrate, “which can hardly be called soil,” lies in alternate valleys and ridges with an average relief of 10 m (Brewer and Triner 1956). Many valleys hold water. Principal trees are Cottonwood, Sycamore, and elm species. Important shrubs are *Rubus*, *Rhus*, *Cornus*, and *Prunus*. Ground cover is sparse. On one strip-mined tract, random pairs of trees were 16–45 m apart (Brewer and Triner *loc. cit.*).

Duration.—In Illinois, tracts probably become habitable by Prairie Warblers about 10 years after stripping, when dense shrubs and woody vines enter (Richard Brewer pers. comm.). Suitable habitat probably lasts 15–20 years (see Brewer 1958), but artificial reforestation would shorten this.

FORESTS AFFECTED BY LUMBERING, FIRE, GRAZING

Location.—Throughout the range, mature forests are lumbered, or burned without lumbering, or lumbered and then burned; grazing may follow. Extent of forest destruction that results is highly variable.

Description.—Michigan example: In a completely cutover scrub-oak area in Crawford County, burned 10 years before study began, all plants were of shrub height; sprouts grew from roots of cut oaks (Walkinshaw *et al.* 1944, Dyer *et al.* 1945, 1946, 1947). Four years later, oaks were closing into dense woods and Prairie Warbler numbers were declining (Walkinshaw pers. comm.). Eastern Kingbirds, Chipping Sparrows, Clay-colored Sparrows, and Field Sparrows were prominent associates of the Prairie Warbler. West Virginia example: An oak forest in Preston County, lumbered 4 or 5 years previously, held a scattering of mature trees (Harrison *et al.* 1962); 60–70% of the area was covered with small deciduous trees and shrubs. The Prairie Warbler was the most abundant bird species; an unusually diverse bird population included woodland forms such as the Eastern Wood Pewee, Black-and-white Warbler, Worm-eating Warbler, and Northern Parula Warbler (see also Murray 1946, 1951, 1961; Cole *et al.* 1961; Hackman 1963). Maryland examples: Disjunct but neighboring plots in a mixed forest had been completely killed by fire 5 years earlier (Stewart *et al.* 1947, Robbins *et al.* 1947). A damp deciduous scrub plot contained Sweet Gum, Red Maple, Black Gum, etc., 2–4 m high; dead tree trunks were still standing. A dry deciduous scrub plot contained oak species, blueberry, Black Gum, etc.; trees were slightly taller than those of the moist plot, and dead trees were no longer standing. The Prairie Warbler was the third commonest bird on the damp plot, the commonest bird on the dry plot; densities were very high (Table 1). Common Yellowthroats, Yellow-breasted Chats, and Rufous-sided Towhees were also very common; House Wrens nested in holes in standing dead trees.

GREAT DISMAL SWAMP

Location.—Virginia, North Carolina.

Description.—A canopied, closed forest was dominated by Red Maple, Swamp Black Gum, Sweet Gum, Tulip, American Holly, Swamp Magnolia, Red Bay; principal shrubs were *Smilax rotundifolia* and *Clethra alnifolia*. Prairie Warblers nested inside the forest, not along the edge as would be expected. Among associated bird species were Prothonotary Warbler, Swainson's Warbler, Hooded Warbler (Brooke Meanley pers. comm., Meanley 1968).

Duration.—Presumably indefinite.

APPENDIX 3

DESCRIPTIONS OF WINTER HABITATS

BAHAMAS

All the information from the West Indies probably pertains to the race *discolor*. In the Bahamas it occurs on nearly every key large enough for a few bushes (Cory 1890: 64-65). In the Biminis it is the second commonest warbler. "Palm Warblers fed on and near the ground, . . . Prairie Warblers in bushes and low trees, and . . . Cape May Warblers in the higher trees" (Mayr 1953).

CUBA

Here it frequents grapefruit and orange groves (Chapman 1918) as well as wild thickets (Barbour 1943: 112). Near Cienfuegos it is found among mangroves, in upland woods, and along borders of wooded streams (Eaton 1953); it occurs in mixed-species flocks, foraging mostly in tops and centers of trees (Eaton *op. cit.*). On the Isle of Pines it frequents low scrub and brush, often remaining hidden and near the ground (Todd 1916: 265).

JAMAICA, HISPANIOLA

On Jamaica the Prairie Warbler inhabits bushes and low woods (Gosse 1847: 159). It is the commonest leaf-gleaning parulid in natural and cutover dry limestone lowland forests, is rare in the mountains. "It takes insects off leaves at the ends of side branches and in the canopy, usually from a perch, but often by hovering" (Lack and Lack 1972: 145). It is typically found in low, scrubby, rather open trees; the average feeding height is 5.3 m (Lack and Lack *op. cit.*: esp. 141-144, 146). On Hispaniola it forages in thickets and low trees, chiefly in the coastal plain and low hills; it avoids the mountainous interior (Wetmore and Swales 1931: 385). It often forages near the ground. When apparently gathering for spring migration, many have been noted in mesquite (Wetmore and Lincoln 1933: 56).

PUERTO RICO

The habitat is about the same as in Hispaniola (Wetmore 1927: 518-520). Some is very dry, including growth just back of beaches, but the species also occurs in pastures with thickets, in low bushes, in hedges, and in coffee fincas; it avoids heavy forest growth (Wetmore *loc. cit.*, Danforth 1925: 121). A few are found in mangroves (Danforth 1930: 129).

VIRGIN ISLANDS

There is a marked association with dry deciduous forest resembling some of the hammocks of the Florida Keys. Prairie Warblers are less often found in moist, open, evergreen hardwood forest with a fairly dense shrub and small-tree stratum (Robertson 1962: 50, 54, 62).

LESSER ANTILLES

On Anguilla the bird has been reported in *Acacia-Croton*-cacti scrub, in vegetation on sandy ridges back of beaches, and in mangroves (Peters 1927).

APPENDIX 4

SIMULATION OF REPRODUCTIVE SUCCESS OF HYPOTHETICAL PRAIRIE WARBLER POPULATIONS, ONE EXPOSED AND ONE NOT EXPOSED TO THE COWBIRD

This appendix presents calculated annual production of fledgling Prairie Warblers by a hypothetical population not exposed to the cowbird and a population exposed to parasitism at the rates observed on the study area. Methods are described on pages 390–393. Table 133 summarizes the results of the calculations.

Every step but the first in each calculation involves applying percentages to numbers carried forward from an earlier step. In order to facilitate reference back to these earlier stages, I have designated each reproductive attempt by a combination of letters and numbers and have indicated in parentheses at each point the prior step to which reference is to be made.

100 FEMALES NOT EXPOSED TO COWBIRDS

I. First-brood attempts

A. 1. Initial nest of season

n = 100 egg 1 date = 14 May % successful = 18%

Results:

successful females = 18, producing 66.80 Prairie Warbler fledglings

unsuccessful females = 82

date of failure = 20 May

% of 82 females replacing failures this date = 94% = 77 females

females leaving their mates = 5

to form new pairs and breed = 5

to quit breeding for year = 0

B. Replacement nests of females still paired with original mate of season

1. First replacement (see I. A. 1., above)

n = 77 egg 1 date = 27 May % successful = 18%

Results:

successful females = 14, producing 50.20 Prairie Warbler fledglings

unsuccessful females = 63

date of failure = 2 June

% of 63 females replacing failures this date = 88% = 55 females

females leaving their mates = 8

to form new pairs and breed = 8

to quit breeding for year = 0

2. Second replacement (see I. B. 1., above)

n = 55 egg 1 date = 9 June % successful = 18%

Results:

successful females = 10, producing 34.30 Prairie Warbler fledglings

unsuccessful females = 45

date of failure = 16 June

% of 45 females replacing failures this date = 78% = 35 females

females leaving their mates = 10

to form new pairs and breed = 6

to quit breeding for year = 4

3. Third replacement (see I. B. 2., above)

n = 35 egg 1 date = 22 June % successful = 24%

Results:

successful females = 8, producing 25.4 Prairie Warbler fledglings

unsuccessful females = 27

date of failure = 30 June

% of 27 females replacing failures this date = 60% = 16 females

females leaving their mates = 11

to form new pairs and breed = 1

to quit breeding for year = 10

4. Fourth replacement (see I. B. 3., above)

n = 16 egg 1 date = 6 July % successful = 27%

Results:

successful females = 4, producing 12.00 Prairie Warbler fledglings

unsuccessful females = 12

date of failure = 18 July

% of 12 females replacing failures this date = 0% = 0 females

females leaving their mates = 12

to form new pairs and breed = 0

to quit breeding for year = 12

C. Nests of females that left original mates: first nest after pairing with new male

1. Females that left males after failure of initial nest of season (see I. A. 1., above)

n = 5 pair formation date = 28 May egg 1 date = 4 June % successful = 18%

Results:

successful females = 1, producing 3.43 Prairie Warbler fledglings

unsuccessful females = 4

date of failure = 11 June

% of 4 females replacing failures this date after midseason pair formation =

41% = 2 females

females leaving their mates = 2

to form new pairs and breed = 1

to quit breeding for year = 1

2. Females that left males after failure of first replacement nest (see I. B. 1., above)

n = 8 date of pair formation = 9 June egg 1 date = 16 June % successful = 22%

Results:

successful females = 2, producing 6.26 Prairie Warbler fledglings

unsuccessful females = 6

date of failure = 24 June

% of 6 females replacing failures this date after midseason pair formation =

31% = 2 females

females leaving their mates = 4

to form new pairs and breed = 1

to quit breeding for year = 3

3. Females that left males after failure of second and third replacement nests (see I. B.

2. and I. B. 3., above)

n = 7 date of pair formation = 23 June and 7 July egg 1 date = 29 June and July 13 % successful = 30%

Results:

successful females = 2, producing 6.13 Prairie Warbler fledglings

unsuccessful females = 5

date of failure = 7 and 25 June

% of 5 females replacing failures this date after midseason pair formation =

15% = 1 female

females leaving their mates = 4

to form new pairs and breed = 0

to quit breeding for year = 4

D. Replacement nests of females that left original mates, built after failure of first nest with new male

1. Females that failed on 11 June (see I. C. 1., above)

$n = 2$ egg 1 date = 17 June % successful = 22%

Results:

successful females = 0

unsuccessful females = 2

date of failure = 25 June

% of 2 females replacing failures this date after midseason pair formation =

32% = 1 female

females leaving their mates = 1

to form new pairs and breed = 0

to quit breeding for year = 1

2. Females that left second mates and paired again (see I. C. 1. and I. C. 2., above) and females that built replacement nests not yet tabulated above (see I. C. 2., I. C. 3., and I. D. 1., above)

$n = 6$ egg 1 date = 24 June and later % successful = 27%

Results:

successful females = 2, producing 6.13 Prairie Warbler fledglings

unsuccessful females = 4

date of failure = 1 July and later

% of 4 females replacing failures this date after midseason pair formation =

15% = 0 females

females leaving their mates = 4

to form new pairs and breed = 0

to quit breeding for year = 4

II. Second-brood attempts

A. Initial attempt

1. Females that succeeded on initial nest of season (see I. A. 1., above)

$n = 14$ (18 \times 80%) date first brood left nest = 7 June egg 1 date = 21 June %

successful = 24%

Results:

successful females = 3, producing 9.39 Prairie Warbler fledglings

unsuccessful females = 11

date of failure = 29 June

% of 11 females replacing second-brood nest failures this date = 30% = 3 females

females leaving their mates = 8

to form new pairs and breed = 1

to quit breeding for year = 7

2. Females that succeeded on first replacement nest (see I. B. 1., above)

$n = 4$ (14 \times 24%) date first brood left nest = 20 June egg 1 date = 4 July %

successful = 24%

Results:

successful females = 1, producing 3.00 Prairie Warbler fledglings

unsuccessful females = 3

date of failure = 16 July

% of 3 females replacing second-brood nest failures this date = 0% = 0 females

females leaving their mates = 3

to form new pair and breed = 0

to quit breeding for year = 3

B. Second attempt with original or new mate

1. Females that failed 29 June (see II. A. 1., above)

$n = 4$ egg 1 date = 4 July and 12 July % successful = 30%

Results:

successful females = 1, producing 3.00 Prairie Warbler fledglings

unsuccessful females = 3

date of failure = 16 July and later

% of 3 females replacing failures this date = 0% = 0 females

females leaving their mates = 3
to form new pairs and breed = 0
to quit breeding for year = 3

100 FEMALES EXPOSED TO COWBIRDS

I. First-brood attempts

A. Initial nest of season

n = 100 egg 1 date = 14 May

% parasitized = 35% = 35 females unparasitized, 35 females parasitized

a. 65 unparasitized females % successful = 18%

Results:

successful females = 12, producing 44.52 Prairie Warbler fledglings

unsuccessful females = 53

date of failure = 20 May

% of 53 females replacing failures this date = 94% = 50 females

females leaving their mates = 3

to form new pairs and breed = 3

to quit breeding for year = 0

b. 35 parasitized females % successful = 7%

Results:

successful females = 2, producing 1.82 Prairie Warbler fledglings and 1.82 cowbird fledglings

unsuccessful females = 33

date of failure = 17 May

% of 33 females replacing failures this date = 95% = 31 females

females leaving their mates = 2

to form new pairs and breed = 2

to quit breeding for year = 0

B. Replacement nests of females still paired with original mate of season

1-1. First replacement nest of females that failed on 20 May (see I. A. 1. a., above)

n = 50 egg 1 date = 27 May

% parasitized = 35% = 32 females unparasitized, 18 females parasitized

a. 32 unparasitized females % successful = 18%

Results:

successful females = 6, producing 21.48 Prairie Warbler fledglings

unsuccessful females = 26

date of failure = 2 June

% of 26 females replacing failures this date = 88% = 23 females

females leaving their mates = 3

to form new pairs and breed = 3

to quit breeding for year = 0

b. 18 parasitized females % successful = 7%

Results:

successful females = 1, producing 0.91 Prairie Warbler fledglings and 0.91 cowbird fledglings

unsuccessful females = 17

date of failure = 30 May

% of 17 females replacing failures this date = 90% = 15 females

females leaving their mates = 2

to form new pairs and breed = 2

to quit breeding for year = 0

1-2. First replacement nest of females that failed on 17 May (see I. A. 1. b., above)

n = 23 egg 1 date = 9 June

% parasitized = 35% = 20 females unparasitized, 11 females parasitized

a. 20 unparasitized females % successful = 18%

Results:

successful females = 4, producing 14.32 Prairie Warbler fledglings
 unsuccessful females = 16
 date of failure = 30 May
 % of 16 females replacing failures this date = 90% = 14 females
 females leaving their mates = 2
 to form new pairs and breed = 2
 to quit breeding for year = 0

- b. 11 parasitized females % successful = 7%

Results:

successful females = 1, producing 0.91 Prairie Warbler fledglings and 0.91 cowbird fledglings
 unsuccessful females = 10
 date of failure = 27 May
 % of 10 females replacing failures this date = 92% = 9 females
 females leaving their mates = 1
 to form new pairs and breed = 1
 to quit breeding for year = 0

- 2-1. Second replacement nest of females that failed on 2 June (see I. B. 1-1. a, above)

n = 23 egg 1 date = 9 June

% parasitized = 25% = 17 females unparasitized, 6 females parasitized

- a. 17 unparasitized females % successful = 22%

Results:

successful females = 4, producing 13.72 Prairie Warbler fledglings
 unsuccessful females = 13
 date of failure = 16 June
 % of 13 females replacing failures this date = 78% = 10 females
 females leaving their mates = 3
 to form new pairs and breed = 2
 to quit breeding for year = 1

- b. 6 parasitized females % successful = 7%

Results:

successful females = 0 (see III, below)
 unsuccessful females = 6
 date of failure = 12 June
 % of 6 females replacing failures this date = 83% = 5 females
 females leaving their mates = 1
 to form new pairs and breed = 1
 to quit breeding for year = 0

- 2-2. Second replacement nest of females that failed on 30 May (see I. B. 1-1. b. and I. B. 1-2. a., above)

n = 29 egg 1 date = 6 June

% parasitized = 25% = 22 females unparasitized, 7 females parasitized

- a. 22 unparasitized females % successful = 18%

Results:

successful females = 4, producing 13.72 Prairie Warbler fledglings
 unsuccessful females = 18
 date of failure = 13 June
 % of 18 females replacing failures this date = 80% = 14 females
 females leaving their mates = 4
 to form new pairs and breed = 3
 to quit breeding for year = 1

- b. 7 parasitized females % successful = 7%

Results:

successful females = 0 (see III, below)
 unsuccessful females = 7
 date of failure = 9 June

% of 7 females replacing failures this date = 85% = 6 females
 females leaving their mates = 1
 to form new pairs and breed = 1
 to quit breeding for year = 0

2-3. Second replacement nest of females that failed on 27 May (see I. B. 1-2. b., above)

n = 9 egg 1 date = 3 June

% parasitized = 25% = 7 females unparasitized, 2 females parasitized

a. 7 unparasitized females % successful = 18%

Results:

successful females = 1, producing 3.43 Prairie Warbler fledglings

unsuccessful females = 6

date of failure = 10 June

% of 6 females replacing failures this date = 83% = 5 females

females leaving their mates = 1

to form new pairs and breed = 1

to quit breeding for year = 0

b. 2 parasitized females % successful = 7%

Results:

successful females = 0 (see III, below)

unsuccessful females = 2

date of failure = 6 June

% of 2 females replacing failures this date = 85% = 2 females

females leaving their mates = 0

3-1. Third replacement nest of females that failed 12-16 June (see I. B. 2-1. a., I. B. 2-1. b., and I. B. 2-2. a., above)

n = 29 egg 1 date = 18-22 June

% parasitized = 10% = 26 females unparasitized, 3 females parasitized

a. 26 unparasitized females % successful = 23%

Results:

successful females = 6, producing 18.78 Prairie Warbler fledglings

unsuccessful females = 20

date of failure = 25-29 June

% of 20 females replacing failures this date = 60% = 12 females

females leaving their mates = 8

to form new pairs and breed = 2

to quit breeding for year = 6

b. 3 parasitized females % successful = 7%

Results:

successful females = 0 (see III, below)

unsuccessful females = 3

date of failure = 21-25 June

% of 3 females replacing failures this date = 64% = 2 females

females leaving their mates = 1

to form new pairs and breed = 0

to quit breeding for year = 1

3-2. Third replacement nest of females that failed 6-10 June (see I. B. 2-2. b., I. B. 2-3. a., and I. B. 2-3. b., above)

n = 13 egg 1 date = 12-16 June

% parasitized = 20% = 10 females unparasitized, 3 females parasitized

a. 10 unparasitized females % successful = 22%

Results:

successful females = 2, producing 6.56 Prairie Warbler fledglings

unsuccessful females = 8

date of failure = 19-24 June

% of 8 females replacing failures this date = 68% = 5 females

females leaving their mates = 3

to form new pairs and breed = 1

to quit breeding for year = 2

b. 3 parasitized females % successful = 7%

Results:

successful females = 0 (see III, below)

unsuccessful females = 3

date of failure = 15-19 June

% of 3 females replacing failures this date = 75% = 2 females

females leaving their mates = 1

to form new pairs and breed = 1

to quit breeding for year = 0

4-1. Fourth replacement nest of females that failed 26-29 June (see I. B. 3-1. a., above)

n = 12 egg 1 date = 1-4 July

% parasitized = 0% = 12 females unparasitized, 0 females parasitized

a. 12 unparasitized females % successful = 24%

Results:

successful females = 3, producing 9.00 Prairie Warbler fledglings

unsuccessful females = 9

date of failure = 13 July-16 July

% of 9 females replacing failures this date = 10% = 1 female

females leaving their mates = 8

to form new pairs and breed = 0

to quit breeding for year = 8

b. 0 parasitized females

4-2. Fourth replacement nest of females that failed 15-25 June (see I. B. 3-2. a. and I. B. 3-2. b., above)

n = 7 egg 1 date = 15-24 June

% parasitized = 3% = 7 females unparasitized, 0 females parasitized

a. 7 unparasitized females % successful = 24%

Results:

successful females = 2, producing 6.56 Prairie Warbler fledglings

unsuccessful females = 5

date of failure = 22 June-2 July

% of 5 females replacing failures this date = 40% = 2 females

females leaving their mates = 3

to form new pairs and breed = 0

to quit breeding for year = 3

b. 0 unparasitized females

5. Fourth replacement nest of females that failed 21-25 June (see I. B. 3-1. b., above) and fifth replacement nest of females that failed 22 June-16 July (see I. B. 4-1. a., I. B. 4-2. a., above)

n = 5 egg 1 date = 27 June-21 July

% parasitized = 1% = 5 females unparasitized, 0 females parasitized

a. 5 unparasitized females % successful = 25%

Results:

successful females = 1, producing 3.07 Prairie Warbler fledglings

unsuccessful females = 4

date of failure = 5 July-2 August

% of 4 females replacing failures this date = 10% = 0 females

females leaving their mates = 4

to form new pairs and breed = 0

to quit breeding for year = 4

b. 0 unparasitized females

C. Nests of females that left original mates: initial nest after pairing with new males

1. Females that left mates after failure of initial nest of season (see I. A. 1. a. and I. A. 1. b., above)

n = 5 pair formation date = 24–27 May egg 1 date = 31 May–3 June

% parasitized = 30% = 3 females unparasitized, 2 females parasitized

a. 3 unparasitized females % successful = 18%

Results:

successful females = 1, producing 3.58 Prairie Warbler fledglings

unsuccessful females = 2

date of failure = 6–10 June

% of 2 females replacing failures this date after midseason

pair formation = 42% = 1 female

females leaving their mates = 1

to form new pairs and breed = 0

to quit breeding for year = 1

b. 2 parasitized females % successful = 7%

Results:

successful females = 0 (see III, below)

unsuccessful females = 2

date of failure = 3–6 June

% of 2 females replacing failures this date after midseason

pair formation = 43% = 1 female

females leaving their mates = 1

to form new pairs and breed = 1

to quit breeding for year = 0

2. Females that left mates after first replacement failed 27–30 May (see I. B. 1-1. a., I. B. 1-1. b., I. B. 1-2. a., and I. B. 1-2. b., above)

n = 8 pair formation date = 3–6 June egg 1 date = 8–11 June

% parasitized = 23% = 6 females unparasitized, 2 females parasitized

a. 6 unparasitized females % successful = 22%

Results:

successful females = 1, producing 3.43 Prairie Warbler fledglings

unsuccessful females = 5

date of failure = 15–18 June

% of 5 females replacing failure this date after midseason

pair formation = 38% = 2 females

females leaving mates = 3

to form new pairs and breed = 1

to quit breeding for year = 2

b. 2 parasitized females % successful = 7%

Results:

successful females = 0 (see III, below)

unsuccessful females = 2

date of failure = 11–14 June

% of 2 females replacing failures this date after midseason

pair formation = 41% = 1 female

females leaving their mates = 1

to form new pairs and breed = 0

to quit breeding for year = 1

3. Females that left mates after second replacement failed 9–16 June (see I. B. 2-1. a., I. B. 2-1. b., I. B. 2-2. a., I. B. 2-2. b., and I. B. 2-3. a., above)

n = 8 pair formation date = 13–23 June egg 1 date = 20–29 June

% parasitized = 12% = 7 females unparasitized, 1 female parasitized

a. 7 unparasitized females % successful = 23%

Results:

successful females = 2, producing 6.26 Prairie Warbler fledglings

unsuccessful females = 5

date of failure = 28 June–7 July

% of 5 females replacing failures this date after midseason pair formation =
30% = 2 females

females leaving their mates = 3

to form new pairs and breed = 0

to quit breeding for year = 3

b. 1 parasitized female % successful = 7%

Results:

successful females = 0 (see III, below)

unsuccessful females = 1

date of failure = 23 June

% of 1 female replacing failure this date after midseason pair formation =

35% = 0 females

females leaving their mates = 1

to form new pairs and breed = 0

to quit breeding for year = 1

4. Females that left mates after replacements other than second failed 15-29 June (see I. B. 3-1. a., I. B. 3-2. a., I. B. 3-2. b., I. C. 1. b., and I. C. 2., a., above)

n = 6 pair formation date = 10 June-6 July egg 1 date = 16 June-12 July

% parasitized = 6% = 6 females unparasitized, 0 females parasitized

a. 6 unparasitized females % successful = 27%

Results:

successful females = 2, producing 6.13 Prairie Warbler fledglings

unsuccessful females = 4

date of failure = 24 June-24 July

% of 4 females replacing failures this date after midseason pair formation =

10% = 0 females

females leaving their mates = 4

to form new pairs and breed = 0

to quit breeding for year = 4

b. 0 parasitized females

D. Replacement nests of females that left original mates and formed pairs in midseason, built after failure of first nest with new male

1. Females that failed 3-18 June (see I. C. 1. a., I. C. 1. b., I. C. 2. a., and I. C. 2. b., above)

n = 5 egg 1 date = 10-24 June

% parasitized = 22% = 4 females unparasitized, 1 female parasitized

a. 4 unparasitized females % successful = 22%

Results:

successful females = 1, producing 3.28 Prairie Warbler fledglings

unsuccessful females = 3

date of failure = 17 June-2 July

% of 3 females replacing failures this date after midseason pair formation =

35% = 1 female

females leaving their mates = 2

to form new pairs and breed = 0

to quit breeding for year = 2

b. 1 parasitized female % successful = 7%

Results:

successful females = 0 (see III, below)

unsuccessful females = 1

date of failure = 15 June

% of 1 female replacing failure this date after midseason pair formation =

39% = 0 females

females leaving their mates = 1

to form new pairs and breed = 0

to quit breeding for year = 1

2. Females that failed 13–29 June (see I. C. 3. a. and I. D. 1. a., above)

n = 3 egg 1 date = 17 June–7 July

% parasitized = 10% = 3 females unparasitized, 0 females parasitized

a. 3 unparasitized females % successful = 24%

Results:

successful females = 1, producing 3.07 Prairie Warbler fledglings

unsuccessful females = 2

date of failure = 25 June–19 July

% of 2 females replacing failures this date after midseason

pair formation = 10% = 0 females

females leaving their mates = 2

to form new pairs and breed = 0

to quit breeding for year = 2

b. 0 unparasitized females

II. Second-brood attempts, with original mate or new mate

A. Initial attempt

1. Females that succeeded on initial nest of the season (see I. A. 1. a. and I. A. 1. b., above)

n = 11 ($14 \times 80\%$) date 1st brood left nest = 7 June egg 1 date = 21 June

% parasitized = 6% = 10 females unparasitized, 1 female parasitized

a. 10 unparasitized females % successful = 24%

Results:

successful females = 2, producing 6.26 Prairie Warbler fledglings

unsuccessful females = 8

date of failure = 29 June

% of 8 females replacing failure of 2d-brood nests this date = 30% = 2 females

females leaving their mates = 6

to form new pairs and breed = 0

to quit breeding for year = 6

b. 1 parasitized female % successful = 7%

Results:

successful females = 0 (see III, below)

unsuccessful females = 1

date of failure = 24 June

% of 1 female replacing failures of 2d-brood nests this date = 32% = 0 females

females leaving their mates = 1

to form new pairs and breed = 0

to quit breeding for year = 1

2. Females that succeeded on first replacement with original mate of season (see I. B. 1-1. a., I. B. 1-1. b., I. B. 1-2. a., and I. B. 1-2. b., above)

n = 4 ($12 \times 30\%$) date 1st brood left nest = 17–20 June

egg 1 date = 1–4 July

% parasitized = 0% = 4 females unparasitized, 0 females parasitized

a. 4 unparasitized females % successful = 24%

Results:

successful females = 1, producing 3.00 Prairie Warbler fledglings

unsuccessful females = 3

date of failure = 13–16 July

% of 3 females replacing failures of 2d-brood nests this date = 5% = 0 females

females leaving their mates = 3

to form new pairs and breed = 0

to quit breeding for year = 3

b. 0 parasitized females

B. Replacement attempt

1. Females that failed 29 June (see II. A. 1. a., above)

n = 2 egg 1 date = 5 July

% parasitized = 0% = 2 females unparasitized, 0 females parasitized

a. 2 unparasitized females % successful = 27%

Results:

successful females = 0

unsuccessful females = 2

date of failure = 17 July

% of 2 females replacing failures this date = 0% = 0 females

females leaving their mates = 2

to form new pairs and breed = 0

to quit breeding for year = 2

b. 0 parasitized females

III. Adjustment to take account of low percentage of success of parasitized nests

n = 28 egg 1 dates = throughout June

Results:

successful females = 2, producing 1.82 Prairie Warbler fledglings and 1.82 cowbird fledglings

APPENDIX 5

PLUMAGE COLORS CHARACTERISTIC OF SEX AND AGE CLASSES

Color terms follow Palmer (1962:4), except that the color "golden" has been added to Palmer's list. Topographic terms follow Palmer (*op. cit.*: 6-7). In applying the color chart to specimens, judgments of several people were obtained to reduce subjectivity. In connection with the following, see frontispiece.

Male in second or subsequent nonnuptial plumage.—Dorsal surface of head, body, wings velvety orange-yellowish olive; very slightly brighter on lower back and rump. Orange-yellowish olive of forehead and crown extends down nape and laterally and anteriorly from nape onto auriculars. From each nostril a golden yellow band runs over eye to posterior edge of eye; these bands merge above base of bill on some males. Below this golden yellow is dull black loreal streak; on some males tips of few of black barbs are yellow. Small spot behind eye, also anterior and posterior edge of eyelid, dull black. Feathers on upper eyelid golden yellow, merging dorsally with band extending backward from nostril. Lower eyelid golden yellow, this color extending ventrally below eye to form large patch there; broad black streak below patch on malar region; on some individuals tips of a few black barbs are yellow. Ventrally, body golden yellow from chin to abdominal region, color extending up sides of head to meet black malar streak and up sides of neck, becoming orange-yellowish olive posterior to malar streak; golden yellow meets under surfaces of wings in axillary region, merges with paler yellow under secondary coverts. Abdominal region yellow, undertail coverts whitish yellow. Sides of breast and belly broadly streaked with black; rows of elongated black spots form streaks that are especially prominent on sides of upper breast.

Female in second or subsequent nonnuptial plumage.—Description is limited to those respects in which the typical old female differs from the typical old male just described. Dorsal surface of head and body slightly less bright than in male, orange-yellowish olive somewhat suffused with gray; color also lacks velvety texture of color of male. Band from nostril to posterior edge of eye narrower than in male and yellow, not golden yellow; loreal streak orange-yellowish olive. Female lacks small spots of dull black behind eye and on anterior edge of eyelid; upper and lower eyelid and patch below eye are yellow; yellow subocular patch considerably larger than that patch on male. Dark malar streak about half width of that of male, and many feathers that are yellow in female are black in male; malar streak of female is dull orange-yellowish olive, not black. Whereas on male color below malar streak is uninterrupted golden yellow, female has narrow golden yellow area, below which is a second streak more or less parallel to malar streak; it is about color of crown. Ventral surface about as in male, but abdominal region paler yellow and undertail coverts paler. Black streaks on sides of breast and belly less conspicuous; particularly, streaks on sides of upper breast are narrower than in male.

Male in first nonnuptial plumage.—Some young males are almost as bright as old males and are distinguishable, if at all, only by (1) grayish tips on black feathers of loreal and malar streaks and (sometimes) on large anterior black spot at side of breast and (2) grayish tips on auriculars. Many young males in autumn resemble the old female, and the following description is limited to differences between these two. General color of dorsal surface darker and grayer than in old female, dull yellowish olive with some feathers or barbs tinged medium gray. Head considerably different than in old female, as follows: Streak beginning at nostril and extending over eye paler yellow and narrower. Both eyelids whitish, tinged very pale yellow, patch below eye same color; on some males only tips of feathers are pale and proximal segments are deeper, brighter yellow. Loreal streak medium gray; feathers sometimes blackish proximally. Malar streak variable; some or all feathers frequently blackish proximally, medium gray distally; general effect grayish. Like adult female, young male has a second streak below malar streak on side of neck, but color is same as that of malar streak. Distal segment of auriculars medium gray to light gray; traces of

these colors sometimes present between posterior edge of eye and auriculars. Ventrally, anterior extremity of interramal region is white, shading posteriorly into yellow, this yellow extending to abdomen. Abdominal region pale yellow; undertail coverts paler than those of adult female.

Female in first nonnuptial plumage.—Description is limited to difference between immature female and immature male. Some young females are as bright and well marked as immature males, but most are grayer dorsally and paler on sides of head and ventrally. General dorsal color close to that of young male, but with more medium gray on lower back. Streak beginning at nostril and running over eye sometimes narrower than in young male, pale gray with no yellowish tones. Upper eyelid very pale gray to white, lower eyelid and patch below eye pale gray. Malar streak medium gray, narrow area below malar streak yellow. Patch on side of neck about color of crown. Auriculars medium gray.

Male in second or subsequent nuptial plumage.—Prenuptial molt produces no changes in color. Abrasion of feathers on mantle makes chestnut patch more conspicuous.

Male in first nuptial plumage.—Prenuptial molt substitutes brighter feathers for some or all of the pale yellow, white, and gray feathers of head and neck; abrasion wears away some pale feather ends. Certain individuals retain conspicuous gray in most of the facial areas that in old birds are black, also are paler yellow and white instead of golden yellow on head and chin. Others retain medium gray and light gray tips on feathers just behind eye and on small area of auriculars (detectable only in hand) but no other characteristics of earlier plumage. Occasional birds believed to be yearlings are in all respects like old males except for more gray in yellow-olive feathers of back, making top of head considerably brighter than back. Museum skins representative of recognizable yearlings include AMNH 383243, USNM N357797, CNHM FM69595, CM 26308, C1 M 38122, UMMZ 110848, ROM 82032.

Female in first nuptial plumage.—Some are same as in previous plumage; at the other extreme, some retain traces of gray only in auriculars; most have some pale yellow and white feathers on chin and around eyes, some gray feathers in loreal stripe, malar streak, and spot on neck. As with yearling males, occasional individuals have frontal and coronal regions noticeably brighter olive than rest of dorsal surface. Museum skins typical of this plumage are AMNH 383258, USNM N124485, CNHM FM150430, C1 M 47010, UMMZ 68814, ROM 7379.

APPENDIX 6

PTERYLOSIS OF THE PRAIRIE WARBLER

Descriptions are based primarily on 10 autumn tower kills (5 of each sex; 6 adult, 4 immature) and 7 molting adults collected near Bloomington, Indiana in August. No sexual differences were detected. I rely heavily on Foster's work (1967a) on the Orange-crowned Warbler and use her language when it is applicable, in order to call attention to similarities and dissimilarities between these two parulids. Quotation marks are omitted. Differences between the pterylosis of the Prairie Warbler and that of the Orange-crowned Warbler are inconsiderable, and Foster's excellent Figures 2 and 3 (*op cit.*: 4, 6) may be consulted in connection with the text that follows.

Alar tract.—Nine well-developed primaries (see lengths in Table 184). Distal and slightly anterior to primary 9 is a feather about 5 mm long and shaped like a primary, which molts in sequence with primaries and is dropped after primary 9; it is obscured by a covert about 6 mm long, slightly above the level of the adjacent row of upper greater primary coverts. On the basis of shape, molt sequence, and position, the small primary-like feather and covert are judged to be vestigial primary 10 and its upper greater covert (compare Foster 1967a).

Nine upper greater primary coverts, including vestigial covert just referred to, are situated dorso-medially between primaries, each proximal to its primary. Greater covert 1 is missing, its site occupied by carpal covert (compare Miller 1928: 398) growing in a lateral and slightly posterior direction. Above greater coverts are 6–7 middle primary coverts; numbers 1 and 9, on some individuals also 2, are missing. A small down feather is located at the base of primary 1 and slightly distal to it; two such feathers are between primary 1 and secondary 1; these are discussed further in connection with upper secondary coverts.

There are nine under greater primary coverts (none for vestigial primary 10), each dorso-medial to its primary, arising from its base and slightly proximally to it; coverts 3–9 emerge from trailing edge of wing, while coverts 1 and 2 are displaced slightly anteriorly. There are either 9 or 10 under middle primary coverts; 1 each arises approximately in line with calami of primaries 1–9; underlying ninth middle primary covert and arising just distally and slightly posteriorly to it is a feather of size, shape, and color of ninth middle primary covert; this may be either a displaced tenth middle primary covert or a marginal covert. One or two small down feathers arise between each two adjacent primaries except primaries 9 and vestigial primary; these molt simultaneously, independently of primaries.

There are nine secondaries (see lengths in Table 184) and nine upper greater secondary coverts, each directly above its secondary. The first seven upper middle secondary coverts arise slightly proximally to corresponding greater coverts. Middle covert 8 arises directly above and in line with secondary 9. What may be a ninth middle covert emerges immediately beside and proximally to ninth greater secondary covert and approaches it in size; this feather is considerably larger than other middle coverts and is displaced to the line of greater coverts.

In addition to upper primary and upper secondary coverts, and distinct from marginal coverts and coverts of patagium, are very small down feathers on trailing edge of dorsal surface of wing (those on either side of primary 1 have been referred to); one and sometimes two each are near bases of secondaries 1–7. These molt on schedule different from that of secondaries, before some of latter have dropped.

Small down feathers arise ventrally between secondaries, almost from trailing edge of wing. These may be under greater secondary coverts (compare Foster 1967a) and are proximal to the respective secondaries, except that ninth (associated with secondary 9) is displaced ventro-anteriorly. There are 8 under middle secondary coverts, each arising just proximally to its secondary; number 9 lacking. There are 9 under lesser secondary coverts; number 1 lies over and slightly distal to middle covert 1; each lesser covert emerges from skin ap-

proximately in line with corresponding secondary. A few small down feathers grow from around bases of lesser and middle coverts of secondaries 7-9.

On alula, three principal feathers are about 14, 10, 6 mm long (anterior to posterior); alular coverts merge proximally with marginal coverts. Marginal coverts extend to humeral tract, merge with it as it passes ventrally over leading edge of wing. Upper lesser coverts on patagium are most numerous in anterior-distal region and on posterior edge of wing. Under coverts, primarily on posterior area of wing, extend sparsely forward to leading edge and proximally to sternal region of ventral tract. Marginal coverts are a narrow band along leading edge of wing.

Caudal tract.—The 12 rectrices are about equally long (see Table 184); central pair is displaced dorsally and lacks upper tail coverts; a covert is directly over each other rectrix. There are 7 pairs of undertail coverts, outer 5 in a row directly beneath rectrices 2-6; next pair is displaced ventrally and slightly toward midline of body, in line with gap between rectrices 1-2; centermost pair is directly under rectrix pair 1 and continues the row formed by coverts 2-6; on 2 individuals 1 or 2 coverts were displaced ventrally 2-3 mm. Several specimens had 1-5 very small yellow down feathers between some or all rectrices.

Anus ringed by single row of feathers (22 on each of 2 specimens), 8-10 mm long at sides of and posterior to vent, gradually decreasing to 3-5 mm anterior to vent. Posterior rim of circlet is broken by narrow gap; within circlet and between this gap and vent are two pairs (sometimes one pair) of feathers whose points of emergence from skin form corners of an approximate square. Small numbers of postventral feathers approach ventro-lateral anal circlet as well as outermost undertail covert.

Capital tract.—Frontal and loreal regions well feathered. Row of three rictal bristles on each side of upper mandible; distal ends of raches of several loreal and interramal feathers lack webs and resemble rictal bristles.

Each loreal region gives rise to about eight widely spaced rows of feathers running across upper eyelid and emerging at its posterior edge. From frontal region arises central coronal area that extends posteriorly to merge with occipital region. Right and left superciliary regions are little differentiated from coronal; it is not clear whether there are coronal apteria (compare Foster 1967a), but a very narrow coronal apterium is visible on nestlings, and one immature male had a small unfeathered area just above posterior section of ocular region. Superciliary region terminates by joining occipital region. Superciliaries appear distinctly separated from ocular feathers on young just acquiring juvenal plumage; superciliary apteria were not seen on immature and adult specimens (compare Foster 1967a).

Occipital region extends postero-laterally around head and bears several filoplumes (about 12 mm), bifurcate or multifurcate distally. Posteriorly occipital region merges with cervical region of spinal tract; laterally it merges with postero-dorsal tip of auricular region, below it with postauricular region. Antero-dorsal to occipital-auricular junctions are small temporal apteria; junctions are also partially bounded on small postauricular apteria, one of which lies on each side of head between auricular region and postauricular region. Each auricular region connects with loreal region antero-ventrally and with ventral ocular feathers antero-dorsally. Each postauricular region runs ventro-anteriorly and joins malar region.

Spinal tract.—Tract arises imperceptibly from posterior occipital region, gradually narrowing and grading into a very narrow interscapular region. Dorsal region arises rather abruptly at level of posterior edge of wing, tends to be wedge-shaped with pointed end toward anterior and opposite end somewhat rounded and of variable width. From each posterior-lateral extremity of base of wedge a single (sometimes double) row of widely spaced feathers runs and meets anterior femoral tract. Truncate band slightly narrower than dorsal region extends posteriorly as pelvic region of spinal tract, then gradually flairs laterally over oil gland.

Humeral tract.—Tract originates ventrally from sternal region of ventral tract, passes dorsally over leading edge of wing, then runs posteriorly to trailing edge where it meets posterior coverts on patagium.

Femoral tract.—Tract is a band, 2-4 feathers wide, running posteriorly around body from level of anterior-pelvic region to level of rectrices; approximately parallel to main axis of body.

Ventral tract.—Well-feathered interramal region gives rise to a central band of feathers, submalar region, which extends posteriorly and then splits into three bands at level of ear; central band continues posteriorly, is much wider than the two on either side of it, which extend postero-laterally. Each distal extension merges laterally with malar region, which arises from undersurface of bill at its lateral extremities and extends posteriorly. Resultant band continues dorsally and connects with postauricular region. At about its midpoint, malar region also merges dorsally with ventral edge of auricular region. Malar and submalar regions are separated on each side by submalar apterium.

Central submalar division extends posteriorly along neck, where it merges with cervical region. Cervical region splits shortly into two ventral-lateral bands, which are weakly differentiated into three regions: Sternal region runs postero-laterally and merges with axillar region, which dips slightly beneath wing and then rises to small peak behind it. Abdominal region, after dipping slightly under thigh, terminates posteriorly at level of anus.

Crural tract.—Posterior surface of the tibia is well-feathered ventrally and dorso-laterally. Sides and medio-dorsal anterior surface are less densely feathered.

APPENDIX 7

MISCELLANEOUS ANATOMICAL AND PHYSIOLOGICAL DATA

Body temperature.—Wetmore (1921: 44) found that the body temperatures of 2 male Prairie Warblers were 107.6°F (42.0°C) and 108.4°F (42.4°C).

Heart weight.—Hartman (1955: 233) reported that a sample of 3 males (weights 7.5, 9.0, and 9.5 g) and 3 females (weights 8.7, 9.0, and 9.0 g) had a mean heart weight 1.24% of body weight. I calculate mean heart weight as 0.11 g, since mean body weight was 8.78 g.

Blood; red corpuscles.—Bartsch *et al.* (1937) measured the red blood cells of the Prairie Warbler; length averaged 10.76 μ and width 6.25 μ . The nuclei averaged 4.93 μ long and 2.13 μ wide.

Blood type.—Robert A. Norris (1963: 25–26), who analyzed the blood of two specimens, kindly sent me data on additional specimens and permission to publish them. An immature of unknown sex, an adult male, and two females (presumably adult) tested negative for antisera anti-A and B. Only the two females were tested for antisera D, K, Fy^a, and P; one female tested positive for P and all other tests were negative. The female positive for P was tested for antisera S and Kp^a, with negative results. The strength of the reactions effecting agglutination was graded on a scale of 0.5 to 5, with 0.5 denoting "very weak" (*op. cit.*: 8). The one positive test, above, graded 0.5.

Stomach lining.—Norris (1961) determined color of stomach linings of various passerines according to three parameters: hue, value, and chroma. When his quantitative readings are converted to his verbal descriptions, one Prairie Warbler's stomach lining was "strong brown."

Bursa of Fabricius.—Russell E. Mumford and I inspected a number of fall tower kills (see p. 439) for the presence of a bursa of Fabricius. We found that structure in 12 of 18 immature autumn males (6 of 10 males killed prior to, and 6 of 8 killed after, 1 September) and 26 of the 36 immature autumn females (16 of 18 females killed prior to, and 10 of 18 killed after, 1 September). Bursas were about 1.5–3.0 mm long and 1.0–2.0 mm in diameter.

Size of gonads.—Mumford and I estimated gonad sizes of many tower kills (see pp. 21, 439). Testis size in spring varied from 4.0 \times 2.7 mm to 2.0 \times 1.6 mm (mean 3.0 \times 1.9 mm). Most testes in autumn were 1.0 \times 0.7 mm or smaller. Within each season, variation in size did not appear to be regularly associated with date, but a male killed on 1 May had testes 5.5 \times 4.5 mm. In autumn, testis size did not vary with age.

In spring the biggest ovaries were 6.5 \times 3.0 mm (width measured across anterior, broadest point), the smallest 3.0 \times 2.0 mm (mean 4.5 \times 2.8 mm). In autumn ovaries of some adults were 3.0 \times 1.7 mm, but most were intermediate between that and the minimum of 1.5 \times 1.0 mm. Ovaries of immatures were 1.5 \times 1.0 mm. We detected no correlation between size and date within each migration period.

Mumford and I collected 2 males in southern Indiana on 4 May, a date when many pairs had formed; 3 testes measured 5.0 \times 3.5 mm and one 2.5 \times 2.0 mm.

Weights.—Weights of migrants are presented in Nolan and Mumford 1965 and Chapter 36, of birds on the winter range on page 18, of dependent young in Chapters 26 and 28.

The weights of 23 adult males caught on my study tract during the breeding season ranged between 8.1 and 6.7 g; the mean was 7.3 g (SD 0.39 g). Three heavily molting birds caught after breeding had ended weighed 7.9, 8.0, and 8.3 g.

Labels of museum specimens occasionally recorded weights. Among males collected in the breeding range in May and June, extremes were 8.3 and 6.4 g; the mean of 13 cases was 7.29 g (SD 0.68 g). Norris and Johnston (1958) report that two adult males collected in summer in Georgia and South Carolina weighed 8.35 and 6.15 g. See also the data used by Hartman in his report of heart weights (above, this appendix).

Weights of 41 females breeding on my study tract ranged from 10.1 to 6.0 g; the mean

was 7.74 g (SD 0.67 g). An additional bird caught about 10 hours before she laid an egg weighed 11.7 g. Doubtless some of the other females contained developing eggs, which would account for the greater variance and the higher maximum weight in females as compared to males. Note that migrant males are heavier than migrant females; see Table 163 and Nolan and Mumford 1965: Table 9.

Weights of six museum specimens from the breeding range in May and June ranged from 9.0 to 6.6 g; the mean was 7.27 g (SD 0.87 g). Norris and Johnston (1958) report that a female taken in summer in Georgia or South Carolina weighed 7.3 g. See also Hartman's data, above.

Abnormalities.—I observed a male, probably a migrant, whose upper mandible was quite thick vertically and curved slightly, like that of a vireo; its tip probably projected beyond the tip of the lower mandible. The bill appeared bilaterally symmetrical, and the bird's foraging seemed normal.

APPENDIX 8

SCIENTIFIC NAMES OF ORGANISMS REFERRED TO IN TEXT ONLY BY VERNACULAR NAMES

Plant nomenclature follows Fernald (1950) except for a few Florida species for which Long and Lakela (1971) was used.

Arthropods are not included in this appendix because they are rarely referred to in the text except by scientific names or by higher categories. Vernacular names are indexed in Borror and DeLong (1971), where their scientific equivalents may be found.

Taxonomy of reptiles follows Dowling (1975). For North American birds, the A.O.U. Check-list (1957) and its supplements were used; Eisenmann (1955) and Witherby *et al.* (1941) provided names for a few species not found in North America. Names of mammals follow Mumford (1969).

PLANTS

fern	Polypodiaceae
pine	<i>Pinus</i> sp.
White Pine	<i>Pinus strobus</i>
Loblolly Pine	<i>Pinus taeda</i>
Long-leaf Pine	<i>Pinus palustris</i>
Slash Pine	<i>Pinus elliottii</i>
Short-leaf Pine	<i>Pinus echinata</i>
Jersey Pine	<i>Pinus virginiana</i>
Pitch-Pine	<i>Pinus rigida</i>
Jack-Pine	<i>Pinus banksiana</i>
cedar	<i>Juniperus</i> sp.
Creeping Juniper	<i>Juniperus horizontalis</i>
Red Cedar	<i>Juniperus virginiana</i>
Purpletop (Tall Redtop)	<i>Triodia flavus</i>
Broomsedge	<i>Andropogon virginicus</i>
sedge	Cyperaceae
Palmetto	<i>Serenoa repens</i>
Maize	<i>Zea mays</i>
Common Greenbrier	<i>Smilax rotundifolia</i>
willow	<i>Salix</i> sp.
Quaking Aspen	<i>Populus tremuloides</i>
Cottonwood	<i>Populus deltoides</i>
Bayberry	<i>Myrica pensylvanica</i>
Black Walnut	<i>Juglans nigra</i>
hickory	<i>Carya</i> sp.
Shagbark Hickory	<i>Carya ovata</i>
Hop-Hornbeam	<i>Ostrya virginiana</i>
oak	<i>Quercus</i> sp.
Chinquapin-Oak	<i>Quercus prinoides</i>
Black Oak	<i>Quercus velutina</i>
Scrub-Oak	<i>Quercus ilicifolia</i>
elm	<i>Ulmus</i> sp.
Slippery Elm	<i>Ulmus rubra</i>
American Elm	<i>Ulmus americana</i>
Hackberry	<i>Celtis occidentalis</i>
Red Mulberry	<i>Morus rubra</i>

Osage Orange
 thimbleweed
 Japanese Barberry
 Swamp-Bay
 Tulip-Poplar
 Red Bay
 Sassafras
 Sweet Gum
 Sycamore
 apple
 crab-apple
 shadbush
 hawthorn
 blackberry
 Wild Plum
 cherry
 Black Cherry
 mesquite
 Honey Locust
 Redbud
 Black Locust
 Smooth Sumac
 Shining Sumac
 Poison Ivy
 American Holly
 Wahoo
 Bittersweet
 Sugar Maple
 Red Maple
 Silver Maple
 Box-Elder
 Ohio Buckeye
 Virginia Creeper
 grape
 Basswood
 cacti
 Red Mangrove
 White Mangrove
 Black Gum
 Swamp Black Gum
 Flowering Dogwood
 Roughleaf Dogwood
 laurel
 huckleberry
 blueberry
 ash
 milkweed
 Black Mangrove
 Buttonbush
 Japanese Honeysuckle
 Coralberry
 goldenrod
 fleabane
 pussy's toes
 dandelion
 thistle

Maclura pomifera
Anemone sp.
Berberis thunbergii
Magnolia virginiana
Liriodendron tulipifera
Persea borbonia
Sassafras albidum
Liquidambar styraciflua
Platanus occidentalis
Pyrus sp.
Pyrus sp.
Ameleanchier sp.
Crataegus sp.
Rubus sp.
Prunocerasus americana
Prunus sp.
Prunus serotina
Prosopis sp.
Gleditsia triacanthos
Cercis canadensis
Robinia pseudo-acacia
Rhus glabra
Rhus copallina
Rhus radicans
Ilex opaca
Euonymus atropurpureus
Celastrus scandens
Acer saccharum
Acer rubrum
Acer saccharinum
Acer negundo
Aesculus glabra
Parthenocissus quinquefolia
Vitis sp.
Tilia americana
 Cactaceae
Rhizophora mangle
Laguncularia racemosa
Nyssa sylvatica
Nyssa sylvatica biflora
Cornus florida
Cornus drummondii
Kalmia sp.
Gaylussacia sp.
Vaccinium sp.
Fraxinus sp.
Asclepias sp.
Avicennia germinans
Cephalanthus occidentalis
Lonicera japonica
Symphoricarpos orbiculatus
Solidago sp.
Erigeron sp.
Antennaria sp.
Taraxacum sp.
Cirsium sp.

REPTILES

Box Turtle
 Eastern Fence Lizard
 Racer
 Rat Snake
 Eastern Hognose Snake
 Milk Snake
 Rough Greensnake
 gartersnake
 Copperhead

Terrapene carolina
Sceloporus undulatus
Coluber constrictor
Elaphe obsoleta
Heterodon platyrhinos
Lampropeltis triangulum
Opheodrys aestivus
Thamnophis sp.
Agkistrodon contortrix

BIRDS

Manx Shearwater
 Sharp-shinned Hawk
 Cooper's Hawk
 Red-tailed Hawk
 Broad-winged Hawk
 American Kestrel
 Bobwhite
 American Woodcock
 Least Tern
 Mourning Dove
 Ringed Turtle Dove
 Yellow-billed Cuckoo
 Black-billed Cuckoo
 Screech Owl
 Great Horned Owl
 Barred Owl
 Whip-poor-will
 Ruby-throated Hummingbird
 Hairy Woodpecker
 Red-cockaded Woodpecker
 Bicolored Antbird
 Eastern Wood Peewee
 Eastern Kingbird
 Great Crested Flycatcher
 Least Flycatcher
 Blue Jay
 Common Crow
 Great Tit
 Black-capped Chickadee
 Carolina Chickadee
 Tufted Titmouse
 Brown-headed Nuthatch
 House Wren
 Carolina Wren
 Long-billed Marsh Wren
 Gray Catbird
 Brown Thrasher
 American Robin
 Wood Thrush
 Eastern Bluebird
 Reed Warbler
 Sedge Warbler
 Blue-gray Gnatcatcher

Puffinus puffinus
Accipiter striatus
Accipiter cooperii
Buteo jamaicensis
Buteo platypterus
Falco sparverius
Colinus virginianus
Philohela minor
Sterna albifrons
Zenaida macroura
Streptopelia risoria
Coccyzus americanus
Coccyzus erythrophthalmus
Otus asio
Bubo virginianus
Strix varia
Caprimulgus vociferus
Archilochus colubris
Dendrocopos villosus
Dendrocopos borealis
Gymnopithys leucaspis
Contopus virens
Tyrannus tyrannus
Myiarchus crinitus
Empidonax minimus
Cyanocitta cristata
Corvus brachyrhyncos
Parus major
Parus atricapillus
Parus carolinensis
Parus bicolor
Sitta pusilla
Troglodytes aedon
Thryothorus ludovicianus
Telmatodytes palustris
Dumetella carolinensis
Toxostoma rufum
Turdus migratorius
Hylocichla mustelina
Sialia sialis
Acrocephalus scirpaceus
Acrocephalus schoenobaenus
Poliophtila caerulea

Pied Flycatcher	<i>Muscicapa hypoleuca</i>
Collared Flycatcher	<i>Muscicapa albicollis</i>
Meadow Pipit	<i>Anthus pratensis</i>
Starling	<i>Sturnus vulgaris</i>
White-eyed Vireo	<i>Vireo griseus</i>
Bell's Vireo	<i>Vireo bellii</i>
Yellow-throated Vireo	<i>Vireo flavifrons</i>
Red-eyed Vireo	<i>Vireo olivaceus</i>
Black-and-white Warbler	<i>Mniotilta varia</i>
Prothonotary Warbler	<i>Protonotaria citrea</i>
Swainson's Warbler	<i>Helmitheros swainsonii</i>
Worm-eating Warbler	<i>Helmitheros vermivorus</i>
Golden-winged Warbler	<i>Vermivora chrysoptera</i>
Blue-winged Warbler	<i>Vermivora pinus</i>
Tennessee Warbler	<i>Vermivora peregrina</i>
Orange-crowned Warbler	<i>Vermivora celata</i>
Nashville Warbler	<i>Vermivora ruficapilla</i>
Northern Parula Warbler	<i>Parula americana</i>
Yellow Warbler	<i>Dendroica petechia</i>
Magnolia Warbler	<i>Dendroica magnolia</i>
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>
Yellow-rumped Warbler	<i>Dendroica coronata</i>
Black-throated Green Warbler	<i>Dendroica virens</i>
Chestnut-sided Warbler	<i>Dendroica pensylvanica</i>
Bay-breasted Warbler	<i>Dendroica castanea</i>
Blackpoll Warbler	<i>Dendroica striata</i>
Pine Warbler	<i>Dendroica pinus</i>
Kirtland's Warbler	<i>Dendroica kirtlandii</i>
Vitelline Warbler	<i>Dendroica vitellina</i>
Palm Warbler	<i>Dendroica palmarum</i>
Ovenbird	<i>Seiurus aurocapillus</i>
Kentucky Warbler	<i>Oporornis formosus</i>
Mourning Warbler	<i>Oporornis philadelphia</i>
Common Yellowthroat	<i>Geothlypis trichas</i>
Yellow-breasted Chat	<i>Icteria virens</i>
Hooded Warbler	<i>Wilsonia citrina</i>
Wilson's Warbler	<i>Wilsonia pusilla</i>
American Redstart	<i>Setophaga ruticilla</i>
Bobolink	<i>Dolichonyx oryzivorus</i>
Redwinged Blackbird	<i>Agelaius phoeniceus</i>
Tricolored Blackbird	<i>Agelaius tricolor</i>
Common Grackle	<i>Quiscalus quiscula</i>
Brown-headed Cowbird	<i>Molothrus ater</i>
Scarlet Tanager	<i>Piranga olivacea</i>
Summer Tanager	<i>Piranga rubra</i>
Cardinal	<i>Cardinalis cardinalis</i>
Indigo Bunting	<i>Passerina cyanea</i>
Chaffinch	<i>Fringilla coelebs</i>
American Goldfinch	<i>Spinus tristis</i>
Canary	<i>Serinus canaria</i>
Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>
Vesper Sparrow	<i>Poocetes gramineus</i>
Bachman's Sparrow	<i>Aimophila aestivalis</i>
Dark-eyed Junco	<i>Junco hyemalis</i>
Tree Sparrow	<i>Spizella arborea</i>
Chipping Sparrow	<i>Spizella passerina</i>
Clay-colored Sparrow	<i>Spizella pallida</i>

Field Sparrow
Song Sparrow

Spizella pusilla
Melospiza melodia

MAMMALS

Opossum
Eastern Cottontail
rabbit
Gray Squirrel
Fox Squirrel
Eastern Chipmunk
Flying Squirrel
Red Fox
Raccoon
Striped Skunk

Didelphis marsupialis
Sylvilagus floridanus
Sylvilagus floridanus
Sciurus carolinensis
Sciurus niger
Tamias striatus
Glaucomys volans
Vulpes fulva
Procyon lotor
Mephitis mephitis

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